

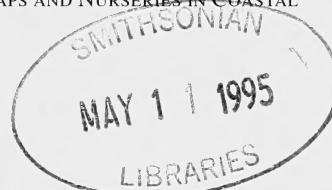


MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$50 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to the treasurer.

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Department of Biology
San Francisco State University
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WIND-SHELTERS AS SAFE SITES FOR ESTABLISHMENT OF *LUPINUS ARBOREUS*, A COASTAL SPECIES

BARBARA L. GARTNER*

Department of Integrative Biology, University of California,
Berkeley, CA 94720

ABSTRACT

To learn the effect of wind on a species native to a windy site, I compared germination, seedling survival, seedling form, and the force required to uproot seedlings in a wind-exposed and a wind-sheltered site. In February 1992, the sand dune perennial *Lupinus arboreus* Sims. was planted in wind-exposed and wind-sheltered plots at Bodega Head, California. Half the individuals were planted from seed and the other half were transplanted from nearby. By late July 1992, 26/43 of the germinants or transplants were still alive in the wind-protected plot but only 3/42 in the wind-exposed plot. This suggests the importance of wind-sheltered sites as safe sites for establishment of this dune species. By 57 days after planting the average plant was smaller in the wind-exposed than the wind-swept plot ($P < 0.05$), but those seedlings that would survive until harvest (day 151) were significantly larger in both plots than those that would die ($P < 0.05$). These data suggest that rapid early growth was important to survival. The wind-exposed survivors at day 151 ($n = 4$) tended to have morphologies more resistant to wind: they averaged twice the stem diameter (2 cm above the ground) and half the height of wind-protected plants ($n = 28$). There were no significant differences in the force required to uproot plants by treatment ($P < 0.05$). Two non-native lupines were also planted from seed to learn how congeners respond to wind. Germination, establishment, and growth of *L. cosentinii* Guss. plants were unaffected by wind, perhaps because the large seed permits rapid development of a taproot to aid in water acquisition. Seedlings of *L. angustifolius* L. cv. Ganja died quickly after total defoliation by caterpillars, suggestive of a major role of chemical defenses for survival of lupines at this sand dune site.

Wind contributes to many aspects of plant form and demography, including growth form, survival, physiology, and dispersal of propagules (Nobel 1981). After asking the effect of simulated wind on the form of tomato plants in a greenhouse (Gartner 1994), I wanted to learn how wind affects the survival, form, and biomechanical function of an undomesticated plant in its native windy habitat.

In response to wind or mechanical stimulation such as rubbing, shaking, or flexing, most plants develop a compact form, with shorter internodes and petioles, and sometimes shorter, thicker, darker epinastic foliage (reviewed in Mitchell et al. 1975; Grace 1977; Jaffe

* Current address and address for reprint requests: Department of Forest Products, Forest Research Laboratory, Oregon State University, Corvallis, OR 97331-7402.

1980; and Biddington 1986). Heiligmann and Schneider (1975) found higher root/shoot dry weight ratios in wind-exposed than wind-protected seedlings of black walnut (*Juglans nigra* L.). Several studies have shown that wind increases allocation to roots, which has been interpreted as a means of increasing a plant's capacity to supply water to the shoot for transpiration (Biddington and Dearman 1985); yet increased root allocation could also result from a shift toward more allocation for anchorage. An optimal plant design to resist lateral forces (such as those induced by wind), is possession of large rigid members near the soil surface (Ennos and Fitter 1992). These rigid members can be a taproot, upper lateral roots, rhizomes, or bases of stems. The response of tomato plants to simulated wind is consistent with Ennos and Fitter's model: increased diameter of the lower stem and upper taproot (Gartner 1994). The taxa in the current study were also taprooted, and I expected to find morphological changes in them similar to those in tomato plants when grown in a wind-exposed habitat compared to a wind-sheltered one.

The current project was undertaken at Bodega Head in northern California, a site with daily strong afternoon winds during late spring and summer. This site was ideal because of its windiness, its abundant *Lupinus arboreus* Sims. (yellow bush lupine), its biological station for weather information and logistical support, and its protection from beach-goers. I chose the species because it is woody (living to a maximum of about 7 years, Davidson and Barbour 1977), thus not switching entirely to a strategy of reproduction at the end of a growing season. Also, it is native to very windy sites, grows well on sand, has an upright form that will catch the wind, and has a non-clonal growth form (Davidson 1975). I also studied two agronomic lupines, *L. cosentinii* Guss. and *L. angustifolius* L., to determine if these plants have the same reaction to wind as the native species.

My hypotheses were 1) that lupines grown in a wind-exposed plot have lower survival than those in the wind-protected site; and 2) that plants in the wind develop shorter, wider stems, and wider taproots than plants in the wind-protected site, and that the force required to uproot the wind-exposed plants exceeds that required to uproot the wind-protected ones. Thus, I expected that plants in windy sites have a form conferring some resistance to overturning by wind, but that they nonetheless would exhibit decreased survival.

MATERIALS AND METHODS

Site. Plants were studied at Bodega Head, in north-central California (latitude 38°18'N, 123°04'W), on the grounds of the University of California Bodega Marine Reserve. Experiments were undertaken during 1992 in a stabilized dune area, with grasses and lupines covering much of the vicinity. The plots were installed on

sparcely vegetated areas that were underlain with many, many roots. The predominant winds blow from the north-northwest, as indicated by the orientation of the dunes. The plots were 400 m downwind from the shore, with their leading edge perpendicular to the predominant winds.

Bodega Head is a windy location. From mid-April to mid-June the mean maximum daily wind-gust velocity was 119 m/sec (1988–1992, measured for 4-second gusts). The July 1991–June 1992 year had about average rainfall (67 cm vs. 74 cm for the 23-year average), although rainfall during the period of seedling establishment was higher than average (39 cm for Feb.–June 1992 vs. 28 cm for that same period in the 23-year average).

Plots. I installed two 7 × 11 m plots, designating the upwind one as wind-exposed and the downwind one (10 m away) as wind-protected. Each plot was surrounded by a 1.8 m high chicken-wire fence (5 cm mesh) designed to exclude rabbits and deer. The base of the fence was buried 10 cm in the sand. The wind-protected plot was then covered with clear plastic sheeting on the leading edge (to a height of 1.8 m) and the right and left sides (to heights of 1.4 m), forming a large U (Fig. 1). To further reduce air motion in the plot, I installed three plastic-covered fences (1 m tall) parallel to the plot's leading edge.

I used a hand-held anemometer (Dwyer Instrument Co., Michigan City, IN) to spot-check windspeeds in the two plots. I recorded the maximum windspeeds on three occasions in 54–78 locations/plot (5-sec periods 20 cm above the ground) and alternated from one plot to the other after each set of four measurements. These measurements were intended to indicate the relative windiness of the two plots, not to quantify the wind itself. Measurements were taken mid-day on 27 May, 7 June, and 30 July. On 20 July, I took five samples of sand from the top 5 cm of each plot for determination of particle-size distribution (using the hydrometer method, Gee and Bauder 1986) and electrical conductivity (using an aqueous substrate paste, Rhoades 1982). Electrical conductivity is an indicator of the substrate's salinity.

The wind-protected plot was less windy than the exposed plot at all times tested (Table 1). The magnitude of wind reduction by the barriers differed by date, probably due to different wind directions, wind speed, and possibly duration (gustiness). The soil substrate did not differ significantly between plots, either in particle-size distribution or electrical conductivity (analysis of variance, $P < 0.05$). Both plots were composed of 99.8–99.9% sand (particles >0.05 mm in diameter) on a dry-weight basis. Electrical conductivity averaged 0.23 ± 0.01 mmho/cm in the exposed plot (mean \pm SE, $n = 5$), and 0.28 ± 0.03 mmho/cm in the protected plot. Therefore, the

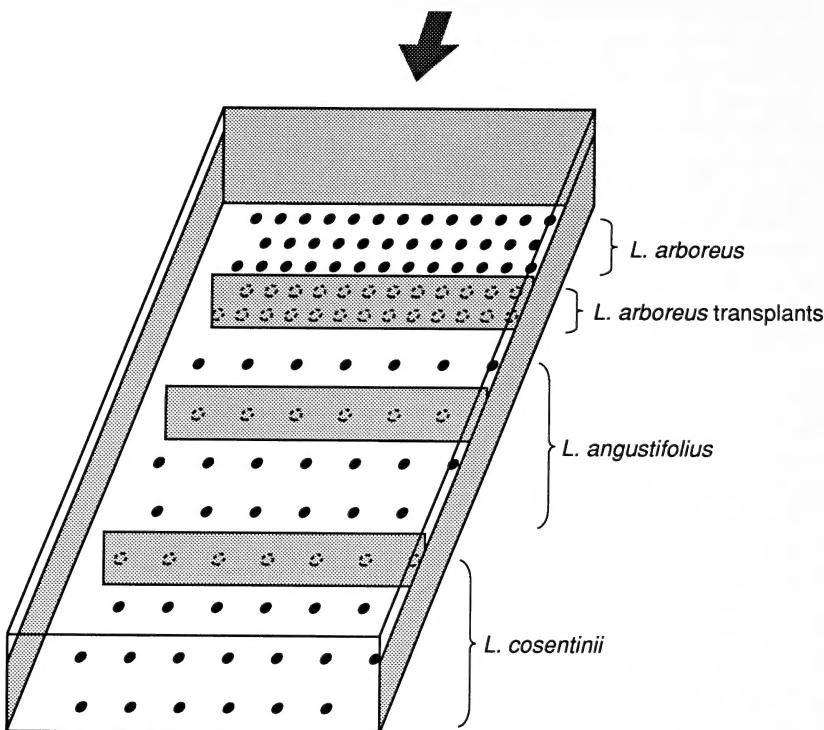


FIG. 1. Diagram of the wind-protected plot showing the predominant wind direction (arrow), 1.8-m tall perimeter fence, plastic barriers (shaded), and locations of seeds or transplants.

plant results I obtained were likely due to the treatments themselves and not to uncontrolled environmental differences.

Cultivation. *Lupinus arboreus* is a perennial shrub native to dunes and the surrounding vegetation at Bodega Head. The *L. arboreus* seeds were collected from Bodega Head the previous year. Both *L.*

TABLE 1. MAXIMUM WINDSPEEDS AT MID-DAY IN 5-SECOND PERIODS (M/SEC, MEAN \pm SE (n); ANOVA).

Measurements/plot (n)	Wind-protected plot	Wind-exposed plot	P
27 May	78	4.7 ± 0.7	<0.01
7 June	54	15.1 ± 1.6	<0.01
30 July	78	2.6 ± 0.6	<0.01

angustifolius and *L. cosentinii* are annual forage plants. Seeds of *L. angustifolius* were obtained from commercial sources and those of *L. cosentinii* were collected from western Australia the previous year. The *L. angustifolius* I studied is an alkaloid-free cultivar (Ganja). In contrast, *L. cosentinii* and *L. arboreus* have high concentrations of alkaloids (B. Bentley personal communication).

On 19 February 1992, I planted the three lupine species in each plot. The first subplot was planted with 38 *L. arboreus* seeds spaced 0.5 m apart. The next subplot had 25 transplanted *L. arboreus* seedlings spaced 0.5 m apart. Several extra seeds were planted in each plot to use as replacements for ones that died. Transplants were taken on a rainy day from within 100 m of the plot. Their seeds had probably germinated within the past 1–2 weeks. Each transplant had cotyledons plus 0–3 leaves. The next two subplots were planted with 26 *L. angustifolius* or *L. cosentinii* seeds spaced 1 m apart, respectively. On April 17 (day 57) I increased the sample size of seedlings to compensate for mortality by including extra seedlings (without moving them) or transplanting recent germinants into the plot (in the seeded and transplanted plots, respectively). These extra seedlings were not used for survival or mortality studies, but were used for biomass and uprooting characteristics. To help seeds germinate and seedlings establish, I watered plots five times between planting and 5 May (day 75). I weeded the plots periodically to remove the volunteer plants that were not part of the study.

Germination, survival, and growth. Survivors were counted on the following days after seeds and transplants were planted: 20 (germinants but not transplants), 57, 97, 108 (*L. cosentinii* only), and 151 (11 March, 13 April, 27 May, 7 June, and 20 July, respectively). Because seeds continued to germinate beyond day 20, I used data from day 53 to calculate the total number of seeds that had germinated (survivors plus standing dead). On day 57 I recorded stem length and number of leaves for each survivor (defined as a plant with green on at least one leaf).

Harvest and force to uproot. I harvested the *L. arboreus* seedlings between 20 and 23 July, 151–154 days after they were planted. Before harvest, I measured the force required to uproot them with a vertical pull at a constant rate of 0.7 mm/sec. The force was provided by a winch mounted on a sawhorse located directly over the decapitated plant (Gartner 1994). A bias-weave sleeve was slipped over the stump of the plant (and affixed with two cable ties). Because of the weave, the sleeve tightens under tension. The sleeve was attached to a spring-scale that was attached to the winch. As I cranked the winch, I watched the spring scale and noted the maximum force before the plant uprooted.

Next, I measured stem length for each *L. arboreus* seedling, and

then stem and taproot diameter every 2 cm. Shoots were then divided into stem or leaf for oven-dry weight determination. I was unable to harvest the roots for dry weight determination because they extended for many meters and intermingled with roots of other plants.

I harvested *L. cosentinii* seedlings on 7 June, 108 days after they were planted. I measured stem length and stem and taproot diameters as described above, then divided plants into stem, leaf, and reproductive tissues for oven-dry weight determination. No *L. angustifolius* plants survived to the harvest date.

RESULTS

Germination, survival, and growth. Seedling survival was higher in the wind-protected plot than in the wind-exposed plot (circles, Fig. 2), but wind had no effect on total germination of *Lupinus arboreus* or *L. cosentinii* (squares, Fig. 2). The data are plotted with absolute numbers of survivors to emphasize sample sizes, but discussed in terms of percentages of total germinants. The survival of *L. arboreus* in the wind-protected plot was 56%, compared to 12% in the exposed plot (Fig. 2A). The difference in survival between plots was even larger for the transplants (64 vs. 4%, respectively; Fig. 2B). For transplants, the early high mortality in the wind-exposed plot suggests that adjustment after transplantation was less successful at the windy site.

The survival of *L. cosentinii* seedlings was slightly higher in the wind-protected than the wind-exposed plot (38 vs. 24%, respectively; Fig. 2C). *Lupinus angustifolius*, the alkaloid-free cultivar, was entirely defoliated, presumably by the larvae of *Platyprepia virginalis* (Lepidoptera, Arctiidae) that were frequently on this lupine. Germination of *L. angustifolius* was higher in the wind-protected than the wind-exposed plot (Fig. 2D) but there were no survivors in either plot 97 days after planting.

For the following size and survival data, I combined data for plants that were introduced as seed and those that were transplanted because they did not differ in size at day 57 or beyond ($P > 0.05$, data not shown). Average plant size was lower in the wind-exposed than wind-protected plot at day 57 (Table 2). However, there was much variation in *L. arboreus* plant size, and its size at 57 days was predictive of its survival to 151 days (harvest date). On the average, survivors had twice as many leaves and were twice as tall at 57 days as those that died before the harvest (Table 3).

Harvest and force to uproot. There were no significant effects of treatment (wind-protection vs. wind-exposure) on plant size at harvest for either species ($P > 0.05$, Table 4). *Lupinus arboreus* tended to be shorter and smaller in the exposed than the protected site, but

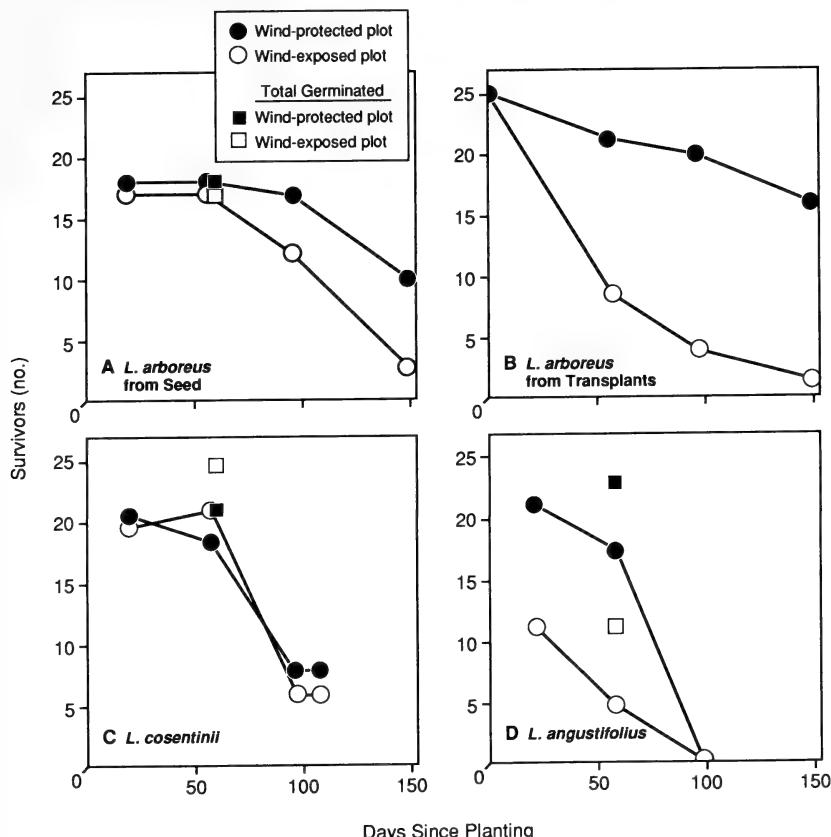


FIG. 2. The number of *Lupinus* survivors at Bodega Head, California, as a function of species and date (circles) in wind-protected vs. wind-exposed plots. Total germination (including standing dead plus survivors) was determined on day 57 (squares). A) *L. arboreus* planted from seed. B) *L. arboreus* germinants transplanted from nearby. C) *L. cosentinii* planted from seed. D) *L. angustifolius* planted from seed.

this was not significant at $P < 0.05$ (Table 4). Sample sizes in Tables 3 and 4 differ because Table 4 includes the extra seedlings that were used to replace some of those that died.

The force required to uproot a plant was quite variable and was not affected significantly by treatment ($P < 0.05$). On average, however, plants in the wind-exposed plot required only 35% of the force

TABLE 2. SIZE OF *LUPINUS ARBOREUS*, DAY 57 (MEAN \pm SE (n); ANOVA).

	Wind-protected plot	Wind-exposed plot	P
Stem length (cm)	2.0 ± 0.4 (39)	1.0 ± 0.2 (26)	<0.01
Leaves (no.)	6.2 ± 0.7 (39)	2.5 ± 0.4 (26)	0.03

TABLE 3. SURVIVAL PREDICTION FOR *LUPINUS ARBOREUS*. Length of stems and number of leaves on day 57 for plants that survived until the harvest (day 151) vs. plants that died before the harvest (mean \pm SE (n); ANOVA).

	Plants surviving to harvest	Plants dying before harvest	P
Stem length at 57 days (cm)			
Wind-protected plot	2.5 \pm 0.4 (26)	1.2 \pm 0.6 (13)	0.09
Wind-exposed plot	2.2 \pm 0.7 (3)	0.9 \pm 0.1 (23)	<0.01
Both plots	2.4 \pm 0.4 (29)	1.0 \pm 0.2 (36)	<0.01
Leaves at 57 days (no.)			
Wind-protected plot	7.2 \pm 0.9 (26)	4.2 \pm 0.8 (13)	0.04
Wind-exposed plot	4.7 \pm 0.9 (3)	2.2 \pm 0.4 (23)	0.06
Both plots	7.0 \pm 0.8 (29)	2.9 \pm 0.4 (36)	<0.01

of those in the wind-protected plot. Force required to uproot a plant/stem cross-sectional area at ground level did not differ significantly between treatments ($P > 0.05$).

DISCUSSION

Protection from wind had no effect on germination but increased seedling survival through the first dry season in *Lupinus arboreus*. Wind-protection increased the number of large plants by day 57 and

TABLE 4. SIZES OF SEEDLINGS AT HARVEST IN THE WIND-PROTECTED AND WIND-EXPOSED PLOTS, FORCE TO UPROOT THEM, AND RATIO OF PROTECTED TO EXPOSED VALUES FOR *LUPINUS ARBOREUS* AND *L. COSENTINII* (MEAN \pm SE; ANOVA).

	Wind-protected plot	Wind-exposed plot	P	Exposed/ protected
<i>Lupinus arboreus</i>				
Shoot DW (g)	(n = 28)	(n = 4)		
Shoot DW (g)	2.3 \pm 0.6	0.2 \pm 0.1	0.23	9%
Stem length (cm)	10.7 \pm 1.9	5.7 \pm 3.3	0.35	53%
Stem or root diameter (mm)				
2 cm above ground	2.2 \pm 0.4	3.9 \pm 1.1	0.15	177%
At root crown	4.0 \pm 0.4	3.1 \pm 0.7	0.44	78%
2 cm below ground	3.3 \pm 0.4	2.4 \pm 0.6	0.40	73%
Force to uproot (kg)	4.0 \pm 0.9	1.4 \pm 0.4	0.30	35%
Force to uproot/stem cross-sectional area at root crown (g/mm ²)	309 \pm 0.46	193 \pm 26	0.36	62%
<i>Lupinus cosentinii</i>				
Shoot DW (g)	(n = 8)	(n = 6)		
Shoot DW (g)	1.2 \pm 0.3	1.3 \pm 0.4	0.79	108%
Stem length (cm)	11.4 \pm 2.2	10.5 \pm 1.0	0.74	92%
Stem or root diameter (mm)				
2 cm above ground	3.7 \pm 0.6	4.0 \pm 0.5	0.67	108%
At root crown	3.5 \pm 0.2	3.8 \pm 0.5	0.63	109%
2 cm below ground	2.5 \pm 0.3	2.7 \pm 0.5	0.71	108%

large plants in either treatment were more likely than small plants to survive from day 57 to day 151, indicating that wind-protection promoted rapid early growth which was important for summer survival. These results also suggest that one dimension of a safe site for seedlings (Harper et al. 1961; Fowler 1988) is the mechanical (Patterson 1992) or wind environment. Previous descriptions of safe sites have listed ranges of such factors as temperature, microtopography, light, and chemical composition of the substrate, but have not underscored the importance of shelter from wind. Nonetheless, the role of wind-shelter in boosting establishment of germinants and transplants has long been recognized in agricultural systems (e.g., Salmon 1916; Heiligmann and Schnieder 1975).

Sites protected from wind appear to be safe-sites for seedling survival, but this study cannot name the factor(s) against which the wind-barrier provides protection: mechanical abrasion, salt, desiccation, or developmental exigencies of living with stem motion (the thigmomorphogenetic response). In one study, dune grass establishment was unaffected by wind alone but was greatly hindered by wind-blown sand that ruptured cells, exposing tissues to desiccation, insects, and pathogens (Fryrear et al. 1973). In the current study wind-blown sand was not apparent because the surface of the study area did not change elevation, although saltation could still have occurred. Sea-salt aerosols (e.g., Ogden 1980) or soil-water salinity (e.g., Okusanya 1979; Lee and Ignaciuk 1985) could have caused the higher mortality and lower growth in the wind-exposed than in the wind-sheltered plot. However, growth and distribution data suggest that *L. arboreus* may be relatively insensitive to salt. In a short-term (15-day) study of foliage burn, *L. arboreus* was less sensitive to salt-spray than two species, and shared the same low level of sensitivity as five other species native to the California strand (Holton and Johnson 1979). *Lupinus arboreus* was abundant in three of the six associations at the strand site, occupying dune swales and mesic slopes up to 30 m from the ocean, and some of its microsites received five times the salt deposition as microsites in which other strand species were restricted (Holton and Johnson 1979).

More likely, the wind-barrier boosted establishment by providing a site where more plants could attain a critical size and then reach the water table throughout the dry season. In contrast, in the exposed site, the stunted growth would have increased vulnerability of plants to drought, and plants would ultimately die of drought stress. It is well-established that wind or simulated wind decreases and qualitatively changes the growth of most dicotyledonous and coniferous species (see reviews in Mitchell et al. 1975; Grace 1977; Jaffe 1980; Biddington 1986; and see Patterson 1992 and Gartner 1994), so it is likely that wind decreased *L. arboreus* growth in the more exposed plot. Moisture stress appears to limit *L. arboreus* establishment: an

earlier study on its demography at Bodega Head implicated herbivory, competition with grasses for light and moisture, and low moisture in general as limitations on seedling establishment (Davidson and Barbour 1977).

The first hypothesis, that plants in wind-exposed sites have lower survival than those in wind-sheltered sites, was supported by the data for the two species that had alkaloids in their tissues, *L. arboreus* and *L. cosentinii*. *Lupinus cosentinii* had low survivorship on both plots and the size of its survivors did not differ significantly by treatment. Even mild water deficits have been shown to decrease net photosynthesis of *L. cosentinii* (Henson et al. 1989). Perhaps the seedlings that were able to become established (regardless of treatment) were those whose taproots reached the water table. Because *L. cosentinii* has larger seeds than does *L. arboreus* (about 220 mg vs. 41 mg/seed, mean of 12 seeds each), seedlings of *L. cosentinii* may have been able to access the water table faster than *L. arboreus*, explaining why wind exposure decreased growth of the *L. arboreus* more than the *L. cosentinii* seedlings.

The alkaloid-free species, *L. angustifolius* was defoliated very soon after germination: there were no live seedlings in either the wind-protected or the wind-exposed site by day 100. The swift disappearance of *L. angustifolius* suggests the effectiveness of chemical defenses in protecting the other lupines from herbivory.

The second hypothesis, that individuals in the wind-exposed plot would have a form more resistant to wind than individuals in the wind-protected plot, was not supported by the data at the significance level $P < 0.05$, although the relative magnitudes of the means for the native species were in the directions predicted by the hypothesis. More survivors are needed to test this hypothesis effectively.

ACKNOWLEDGMENTS

I am thankful to Barbara Bentley for providing the seeds; to Barbara Bentley and Mimi Koehl for discussions and suggestions along the way; to Vic Chow for weather data; to Art and Edie Lachenbruch, Kevin Gartner, and Susan Harrison for field help at a few crucial periods; to Steve Radosevich and two anonymous reviewers for comments on the manuscript; and to Peter Connors and others at the Bodega Marine Laboratory and Bodega Marine Reserve for helping facilitate my study and for making the lab a hospitable working site. This is Paper 2967 of the Forest Research Laboratory, Oregon State University, Corvallis, OR 97331.

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(Received 27 Sep 1993; revision accepted 16 Aug 1994)

ERIGERON BISTIENSIS (ASTERACEAE: ASTEREAE):
A NEW SPECIES FROM NORTHWESTERN NEW MEXICO

GUY L. NESOM

Department of Botany, University of Texas, Austin, TX 78713

BILL HEVRON

Navajo Natural Heritage Program, P.O. Box 1480,
Window Rock, AZ 86515

ABSTRACT

Erigeron bistiensis Nesom & Hevron is described and illustrated. It is presently known from a single population in San Juan County, New Mexico. The new species is a member of the *E. compactus* group of sect. *Wyomingia* and is very similar to *E. untermannii* from northeastern Utah. The concept of *E. untermannii* is broadened to include *E. carringtoniae*.

Recent intensive collecting in northwestern New Mexico continues to bring new taxa to light. The species of *Erigeron* described here is among the rarest in New Mexico.

Erigeron bistiensis Nesom & Hevron, sp. nov. (Fig. 1).—TYPE: USA, New Mexico, San Juan Co., Navajo Indian Reservation, San Juan Basin NE of Bisti Trading Post, 4.2 mi E of New Mexico Hwy 371, ca. ¼ mi S of San Juan Co. Rd. 7250, ridge tops and slopes of Hunter Wash drainage in desert shrub–grassland, T25N, R12W, S31 NE ¼, NE ¼ [New Mexico 7.5' USGS quadrangle = Alamo Mesa West], 6340 ft, most plants past flowering or with withered rays, 5 June 1993, Bill Hevron 1975 with J. Merz (holotype: UNM; isotypes: ARIZ, ASC, ASU, BRY, COLO, NMC, NY, TEX, UC, US, UT, UTC).

A *Erigeronti compacto* Blake et speciebus affinibus similis habitu pulvinato radice palari, ramis caudicibus numerosis crassis ascendibusque, vestimento albi-strigilloso, foliis angustis, floribus radiis ligulis circinnatis, et acheniis complanatis 2-nervatis; inter has species *E. untermannii* Welsh & Goodrich maxime similis sed caulis 2–3 cm altis, foliis dense strigillosi-cinereis linearibus vel anguste oblanceolatis non redactisque in dimidio inferiore caulum, capitulis minoribus, et acheniis faciebus dense sericeis nervis aurantiaci-resinaceis dignoscenda.

Caespitose, perennial herbs arising from a thick taproot with numerous, short (1–4 cm long), ascending-erect caudex branches, forming clumps up to 30 cm in diameter. Stems erect, 7–15 cm tall,



FIG. 1. Habit of *Erigeron bistiensis* (from TEX isotype).

unbranched, gray-green, moderately to densely strigose with white, stiff, appressed hairs 0.1–0.5 mm long, eglandular. Leaves gray-green, similar in vestiture to the stems, in dense basal clusters from the caudex apices, mostly erect, linear to linear-ob lanceolate, entire, 10–25 mm long, 1–2 mm wide, slightly broadened at the very base, the cauline sessile, ascending and continuing relatively unreduced in size $\frac{1}{2}$ – $\frac{3}{4}$ up the stems. Heads solitary, terminal, cupulate, 11–16 mm wide (pressed); phyllaries in 2–3 (–4) subequal series, 5–7 mm long, narrowly oblong-lanceolate, evenly loosely short-pilose, minutely but prominently granular-glandular. Ray flowers 30–40 in a single series, the corollas 8–13 mm long, ligules 1.5–2.0 mm wide, white, drying white or pinkish to bluish, distinctly coiling from the apices with maturity. Disc corollas 3.8–4.5 mm long, narrowly funnelform, not strongly indurated or inflated, glabrate; style branch collecting appendages deltate to shallowly triangular, 0.2–0.3 mm long. Achenes with 2, orange-resinous nerves, oblong-obovate, 2.5–3.0 mm long, 0.6–1.0 mm wide, the faces and margins densely

strigose-sericeous; pappus of 32–39 barbellate bristles ca. $\frac{2}{3}$ the disc corolla height, with a few outer setose bristles 0.5–1.0 mm long. Known only from the type locality, the epithet is in reference to the immediately adjacent BLM Bisti–De Nazin Wilderness Area.

Additional collection examined: New Mexico, San Juan Co., type locality, heads immature, just beginning to flower, 3 May 1991, *Hevron 1145* (TEX, UNM).

DISTRIBUTION AND HABITAT

Erigeron bistiensis is locally abundant on the highly dissected, south-trending slopes in the upper stratigraphic portion of the Hunter Wash drainage (Fig. 2). The substrate is a white to tan, fine-textured sand immediately derived from the Cretaceous Ojo Alamo Sandstone formation (Dane and Bachman 1965). This formation is located between the brown-red sand of the upland grassland and the gray clay badlands of the Kirtland formation at lower elevations. The new species is restricted to ridge tops and slopes of the Ojo Alamo but was not observed in arroyo bottoms. Plants were noted from all aspects on slopes of 0–30 degrees. At the type locality, about 200–250 plants of *Erigeron bistiensis* are scattered over 3–4 acres along the Ojo Alamo formation, which extends for approximately 100 yards into the Hunter Wash drainage.

The Ojo Alamo formation extends northwestward from the Hunter Wash area for about 30 miles in a narrow (mostly 1–3 km wide), continuous arc roughly paralleling the Chaco River to the San Juan River in the vicinity of Farmington, New Mexico. This city lies on the most sizable expanse of exposed Ojo Alamo Sandstone and urban development may have eradicated the largest amount of suitable habitat potentially available for *Erigeron bistiensis*. North of the San Juan River, the Ojo Alamo occurs sporadically for a short distance. Eastward from the Hunter Wash area, the Ojo Alamo continues in a narrow band for approximately 90 miles, extending into northwestern Sandoval County to the vicinity of Cuba.

The desert shrub-grassland of the type locality is characterized by the following species: *Ephedra torreyana* S. Wats., *Oryzopsis hymenoides* (R. & S.) Ricker, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Steud., *Leptodactylon pungens* Nutt., *Hilaria jamesii* (Torr.) Benth., *Stipa comata* Trin. & Rupr., *Yucca angustissima* Engelm. & Torr., *Astragalus praelongus* Sheldon, *Astragalus ceramicus* Sheldon, *Dalea candida* (Michx.) Willd., *Ericameria nauseosa* (Pallas ex Pursh) Nesom & Baird, *Machaeranthera grindeliaoides* (Nutt.) Cronq., *Hymenopappus filifolius* Hook., and *Tetradymia canescens* DC.

There were no signs of predation, herbivory, or disease on *Erigeron bistiensis*. Grazing is intense in the area of the type locality, but livestock do not appear to pose a threat to the continued existence

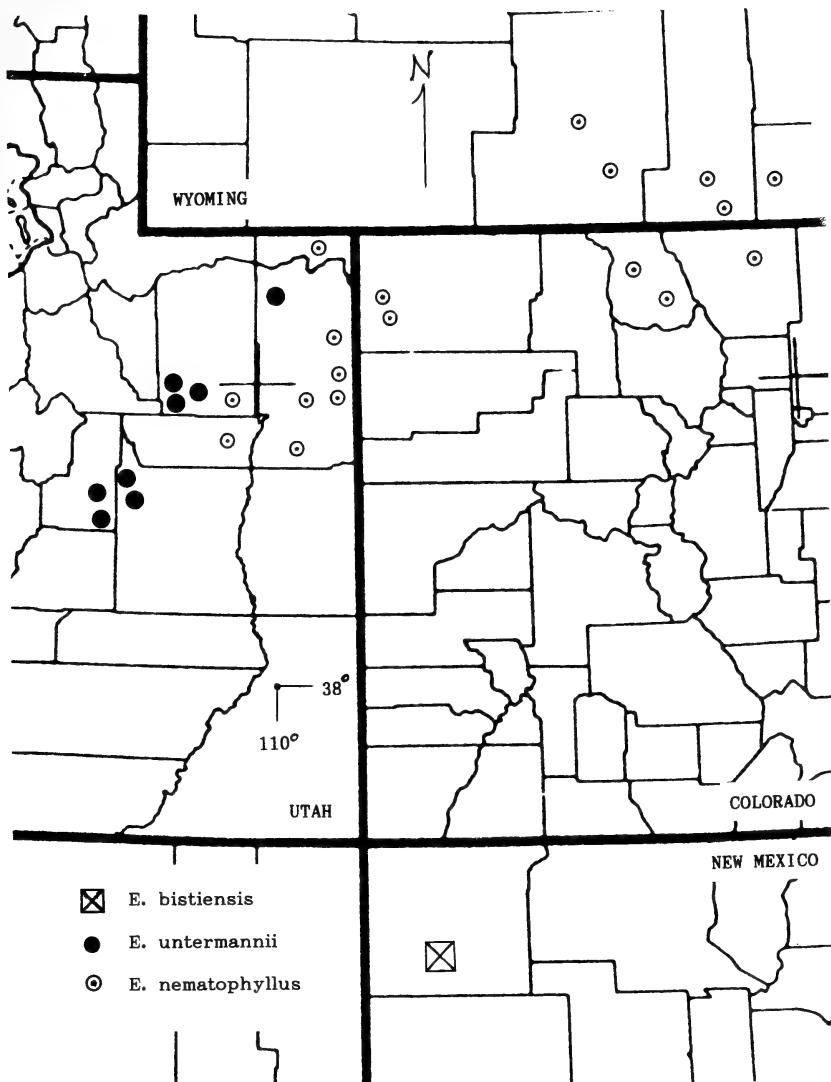


FIG. 2. Distribution of *Erigeron bistiensis* and the similar species *E. untermannii* and *E. nematophyllus* (see comments in text).

of the species, which appears to be relatively unpalatable. Oil and gas extraction, with associated road construction, represents the other major land use and may pose a significant threat. Based on its small population size and current threats, *E. bistiensis* will be proposed as a candidate for listing under the Endangered Species Act.

INFRAGENERIC POSITION

Erigeron bistiensis is a member of the *E. compactus* Blake group of sect. *Wyomingia* (A. Nelson) Cronq. (sensu Nesom 1989) in its taprooted, pulvinate habit with numerous, thick, ascending caudex branches, white-strigillose vestiture, narrow leaves, coiling ligules, and flattened, 2-nerved achenes. The discovery of this species further emphasizes the distinctiveness of the *E. pulcherrimus* Heller group within sect. *Wyomingia*, which differs in its multi-nerved achenes from the *E. compactus* group as well as the rest of the genus. *Erigeron bistiensis* is the second recently discovered species of the *E. compactus* group from northwestern New Mexico. The first, *E. sivinskii* Nesom (Nesom 1991), is distinguished from *E. bistiensis* by the following contrasts:

1. Stems and leaves grayish, moderately to densely short-strigose; leaves mostly narrowly oblanceolate, 1–2 mm wide at widest point; phyllaries canescent with ascending-appressed hairs, midvein relatively broad and orange-resinous; disc corollas 3.8–4.5 mm long; achenes oblong-obovate, the faces densely strigose-sericeous; pappus of 32–39 bristles; San Juan Co. *E. bistiensis*
1. Stems and leaves greenish, sparsely short-strigose; leaves linear, 0.6–0.8 wide at widest point; phyllaries sparsely pilose-hispid with spreading hairs, midvein relatively thin and yellowish; disc corollas 3.0–3.8 mm long; achenes oblong, the faces glabrous; pappus of 21–27 bristles; McKinley Co. *E. sivinskii*

Within the *Erigeron compactus* group, *E. sivinskii*, *E. compactus*, and *E. consimilis* Cronq. constitute a group marked by the production of achenes with completely glabrous faces but strigose or sericeous margins (Nesom 1991), a distinctive feature otherwise rare within the genus. The remaining members of the *E. compactus* group, *E. bistiensis*, *E. untermannii* Welsh & Goodrich, and *E. nematophyllum* Rydb. (Fig. 1), produce achenes with markedly hairy faces and margins. Among these species, *E. bistiensis* and *E. untermannii* are similar to each other in their strongly foreshortened, densely pulvinate habit and grayish vestiture, but the new species is separated from the closest populations of *E. untermannii* by a distance of about 450 kilometers, and the two species are clearly distinguished morphologically. They are included in the following key (adapted and extended from Nesom 1991), which separates all of the species of the *E. compactus* group.

1. Leaves mostly (2–) 4–8 cm long, the lower margins ciliate, persistent portion of old basal leaves relatively long and slender-fibrous; sw Wyoming, w Colorado, ne Utah *E. nematophyllum*
1. Leaves mostly 1–3 cm long, margins eciliate, persistent portion of old basal leaves short and broad (2)
 2. Achenial faces and margins strigose or strigose-sericeous (5)
 2. Achenial faces glabrous, the margins sparsely to densely ciliate (3)
 3. Stems, leaves, and phyllaries green, sparsely short-strigose; stems with relatively unreduced leaves on at least the lower half; phyllaries relatively

thin-herbaceous; achene margins sparsely ciliate; nw New Mexico *E. sivinskii*

3. Stems, leaves, and phyllaries gray-green, densely short-strigose; stems essentially scapose, sometimes with a few, small, scattered bracts; phyllaries distinctly thickened along the margins; achene margins densely ciliate (4)

4. Phyllaries spreading-hispidulous with thick-based trichomes; heads 15–20 mm wide; rays 30–55; w Colorado, e Utah, ne Arizona *E. consimilis*

4. Phyllaries strigose with thin-based trichomes; heads 8–15 mm wide; rays 15–32; e California, Nevada, w Utah *E. compactus*

5. Leaves mostly narrowly oblanceolate, the blades 1–2 mm wide, caulin leaves essentially unreduced $\frac{1}{2}$ – $\frac{3}{4}$ of the distance up the stem; heads 11–16 mm wide; rays 30–40, the ligules 8–13 mm long; achenes densely sericeous, with orange-resinous nerves; pappus bristles 32–39; nw New Mexico *E. bistiensis*

5. Leaves oblanceolate to spatulate, the blades 2–7 mm wide, caulin leaves absent or few and restricted to the lower $\frac{1}{4}$ of the stem; heads 7–12 mm wide; rays 18–30, the ligules 5–10 mm long; achenes moderately strigose, with light-colored nerves; pappus bristles 18–26; nw Utah *E. untermannii*

Erigeron untermannii is considered here to include *E. carringtoniae* Welsh. In the original description of the former, Welsh (1983a) compared it with *E. compactus*, observing that his new species differed from the latter in broader leaves with ascending to spreading hairs and in shorter ray corollas. He noted that *E. carringtoniae* differed from *E. untermannii* in its involucral bracts with longer, thinner hairs and longer ray corollas. The same differences were also used to distinguish the latter two taxa in his key to Utah *Erigeron* (Welsh 1983b). With a broader selection of collections at hand (20 of *E. untermannii*, 9 of *E. carringtoniae*, as identified at BRY, representing a total of ca. 68 plants; the majority of these collections made since 1989), we cannot find any morphological feature that would separate the two taxa. The populations in Sanpete and Emery counties occur on the Wasatch Plateau at elevations of 3000–3300 meters, compared to those in Duchesne and Uintah counties, which are along the margin of the Uintah Basin at 2175–2835 meters, but all of them occur in relatively exposed habitats on substrates of shale, limestone, or marly gravel.

ACKNOWLEDGMENTS

We thank the staff of BRY for a loan of the types and general collections of *Erigeron untermannii* and *E. carringtoniae*, the anonymous journal reviewers for their comments, and S. Milligan for the illustration. The distribution map was drawn from specimens from TEX and BRY, with the addition of data for *E. nematophyllum* from Albee et al. (1988) and Cronquist (1947).

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(Received 15 Nov 1993; revision accepted 15 Sep 1994)

ANNOUNCEMENT

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OBSERVATIONS ON *PINUS MAXIMARTINEZII* RZED.

JEFFREY K. DONAHUE

CAMCORE Cooperative, Dept. of Forestry,
North Carolina State University, Box 7626,
Raleigh, NC 27695-7626, USA

CARLOS MAR LOPEZ

Grupo GENFOR, Apdo. Postal 152, Chapingo, Edo. Méx. 56230,
México

ABSTRACT

Pinus maximartinezii is a rare pinyon pine with a natural range restricted to one site in the state of Zacatecas, Mexico. Based on recent field reconnaissance, the entire distribution has been determined to be approximately 400 hectares. The species' altitudinal distribution is 1600 to 2550 meters above sea level. The population size is estimated to be approximately 2000 to 2500 mature individuals. Observations on the species' reproductive cycle and site and soil characteristics are included in this report.

RESUMEN

Pinus maximartinezii es un pino piñonero muy escaso, con una distribución natural restringido a un solo sitio en el estado de Zacatecas, México. En base a un reconocimiento reciente del sitio, se ha determinado que el área total de la población es aproximadamente 400 hectáreas. La especie crece entre 1600 y 2550 metros sobre el nivel del mar. Se estima que el numero total de individuos de edad reproductiva es entre 2000 y 2500. Este reporte incluye observaciones del ciclo reproductivo y de las características del sitio y de los suelos.

Pinus maximartinezii Rzed. is a Mexican pinyon pine reported growing only in the state of Zacatecas. One of the least known of the Mexican pines, it is considered rare and endangered because of its restricted distribution and small population size (Rzedowski 1964; Perry 1991). In fact, Styles (1993) considered it one of the most threatened of all pine species.

This species has leaves in fascicles of five, 7–11 cm in length, with 2 external resin canals. It is one of only two five-needle pinyon pines in North America. Cotyledons number from 18 to 24, a unique trait among conifers, which usually have a maximum of eighteen (Rzedowski 1964). Female cones average 15–23 cm in length and 11–13 cm in diameter, with some attaining 30 cm in length and 18 cm in diameter. The mature seed cones are similar in form and size to those of *P. coulteri* D. Don, and may reach a green weight of 1½ to

2 kg. The cone scales are unique among pinyon pines, being very large, thickened, and extremely hard upon drying. Oleoresin monoterpane content is about 90% limonene, as in *P. pinceana* Gordon (Zavarin and Snajberk 1987). Complete descriptions of this species are given by Rzedowski (1964), and Perry (1991). This is the first report containing information on strobili development and timing.

The taxonomic classification of *Pinus maximartinezii* is still in doubt. Little and Critchfield (1969) placed it in subsection *Cembroides*. Considered a relict species, *P. maximartinezii* is most closely related to *P. pinceana* and *P. nelsonii* Shaw (Bailey and Hawksworth 1987; Malusa 1992). Because of morphological differences between *P. maximartinezii* and *P. pinceana* and the other taxa in *Cembroides*, Rzedowski (1964), and Bailey and Hawksworth (1987) suggested that a new subsection be created for these two species. Perry (1991), in his revised classification of the Mexican pines, placed both *P. maximartinezii* and *P. pinceana* in a new subsection *Pinceana*. Malusa (1992) thought both species more closely related to subsection *Gerardiana* than to *Cembroides*.

The objective of this account is to report on the distribution of *Pinus maximartinezii*, and provide new information on its reproductive cycle and the environment in which it grows. Information on the species' reproductive cycle is reported as observed in its native environment. Studies in planted trials will be important in providing more complete details on the biology of this species.

The information reported here was collected in February and June of 1993, as part of a gene conservation project in which the species' distribution was mapped, the site characterized, and individual trees selected for seed collections.

POPULATION SIZE AND SITE CHARACTERISTICS

The only known population of *P. maximartinezii* is on Cerro Piñones at the southern extreme of the Sierra de Morones, Zacatecas ($21^{\circ}22'N$, $103^{\circ}14'W$) (Fig. 1), at 1600 to 2550 m. Most of the population occurs in a band from 2100 to 2300 m elevation. Elevations were measured with a mechanical pocket altimeter, and corroborated with topographic charts.

The species total range is about 400 hectares (Fig. 1). The pine grows on the eastern, southern and southwestern aspects of Cerro Piñones, but not on the mountain 1 km to the north. The range was determined by field reconnaissance and measurements on a 1:50,000 topographic chart with an electronic planimeter.

The pines comprise two subpopulations, separated by a ridge top, but not completely isolated reproductively from one another; one on the east slope, and the other on the southwestern slope. On the east slope, groups of 3 to 5 trees predominate, situated mainly in

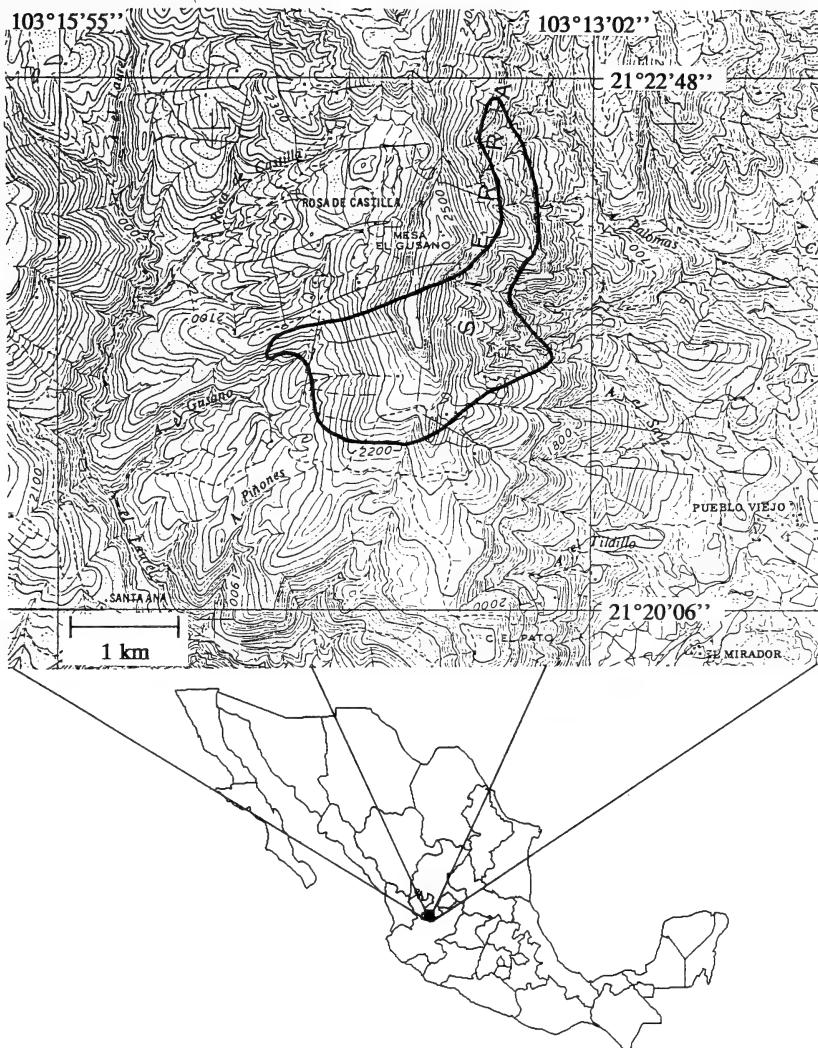


FIG. 1. Distribution of *Pinus maximartinezii* on Cerro Piñones, Zacatecas, Mexico. Based on Topographic Chart 1:50,000 Juchipila F-13-D-36, Instituto Nacional de Estadística Geografía e Informática (Mexico), 1973.

and along the draws. This spatial arrangement is probably due to past felling for grazing activities. Isolated individuals (>100 m to nearest neighbor) are widely scattered. On the southwest slope, although fewer in number, the pines are denser, with groups of 10 to 30 trees and distances of 10 to 50 m among trees. Based on our observations, the total number of mature trees is about 2000 to 2500.

The site where *P. maximartinezii* grows receives an estimated 800–900 mm annual rainfall, most of which falls in June through September (SARH 1988). Malusa (1992) called this the highest rainfall for any pinyon pine in North America. The mean annual temperature is about 17°C. Climatic estimates are based on data collected at the Juchipila, Zacatecas, meteorological station.

Soils on Cerro Piñones where the pines grow are calcareous, and limestone and gypsum outcrops are abundant on the eastern slopes, specifically along the southern ascent route. Near the northeastern extreme of the pines' extension, a loose reddish igneous rock (scoria) is scattered about the surface. Here the woody vegetation changes from pine–oak to mixed hardwoods, suggesting that *P. maximartinezii* may be restricted to the calcareous soils on the southern extreme of this mountain. According to Malusa (1992) *Pinus nelsonii*, *P. pinceana* and *P. johannis* Robert, other locally endemic Mexican pinyons are limited to calcareous soils.

We collected soil samples at 10 cm depth, from four places on east, west, and west-southwest slopes where the pines grow. The two eastern slope samples were sandy clays and sandy clay loams, with a pH of 7.2 and 7.5. Samples from the west and west-southwest slopes were both clay loams, with a pH of 7.0 and 6.8. Soil reactions were field tested and recorded with a pocket digital pH meter. Textures were determined in the field by the tactile method.

REPRODUCTIVE CYCLE

On February 17, 1993, we found two distinct female cone crops on the trees. The smaller cones were about 4–6 cm long, and 3–5 cm in diameter, apparently still growing. The larger cones appeared nearly mature (about 15–20 cm long and 10–12 cm diameter), with resin exudations beginning to appear on the cone scales. We saw no new, emerging female cones. A few very sporadic male strobili were beginning to emerge. This information on strobili development is based on observations of 100 trees growing in natural stands, which were selected for seed collection.

Four months later, on June 15, 1993, we found new female cones about 1–2 cm long and 1 cm in diameter, that had apparently just passed the receptive stage. The female cones emerge solitarily at the ends of the branches. Empty male strobili were still attached to the branches, but pollen dispersal had clearly ended across the site. Cones of the intermediate crop were now about 6–8 cm in length. The largest cones were now more completely covered with resin exudations, and the cone scale apophyses had begun to turn brown. Thus we saw three distinct cone crops on the trees at the same time, indicating a reproductive cycle spanning four growing seasons from reproductive bud initiation to cone maturity.

Reproductive bud initiations in *P. maximartinezii* probably occur between August and September. Pollination apparently is in May and/or June of the second year. The exact time lapse between pollination and fertilization is unknown, but fertilization probably occurs in either the second or third year, rather than the fourth. Cone maturation and seed dispersal take place in September and October. A similar cycle has been reported for *P. leiophylla* Shiede and Deppe, *P. torreyana* Parry ex Carr. and *P. pinea* L. (Martínez 1948; USDA Forest Service 1974; Owens and Blake 1985), and likewise for *P. chihuahuana* Engelm. (Mirov 1967; Perry 1991), which some authors consider a variety of *P. leiophylla*.

In most pine species with a three-year reproductive cycle, fertilization is twelve to fourteen months after pollination. Owens and Blake (1985) wrote that in pines with a four-year reproductive cycle, pollination takes place in the second year, but pollen tube and ovule development remain arrested for two years, with fertilization, and embryo and seed maturation occurring in the fourth year (Table 1). This is unlikely with *P. maximartinezii* because the largest seed cones were already fully elongated and nearly mature in February, eight months prior to seed dispersal, with external resin exudations, indicating that fertilization had occurred in a previous year. Apparently this species undergoes a prolonged period of cone development and maturation. Having the largest cones and seeds of the pinyon pines (and among the largest for all pines), it is possible that *P. maximartinezii* needs an extended period after fertilization to produce them because of the short 4–5 month growing season at the site where it occurs. If this is true, fertilization could occur a few weeks after pollination, in the second year, or twelve months later, in the third year (Table 1). Cones would mature and disperse seeds in the fourth year.

Therefore, in June, at the time of our second field observation, the largest cones would have been in their fourth year from time of bud initiation, the 6–8 cm cones would have been third-year, and the 1–2 cm conelets second-year. Strobili development and seed dispersal dates for *P. maximartinezii* nearly coincide with those of *P. edulis* Engelm. and *P. monophylla* Torr. and Frem. in the USA (USDA Forest Service 1974).

CONSERVATION

The remaining pines grow on private property. The landowners value them for the pine nuts, and try to conserve the mature, fruiting trees. Natural regeneration was sparse in 1993, possibly because of continued cattle grazing on the site, and a ground fire that occurred in 1989. Several old mature trees were killed by the fire, apparently their relatively thin bark unable to tolerate high temperatures.

TABLE 1. A COMPARISON OF THREE AND FOUR-YEAR PINE REPRODUCTIVE CYCLES WITH THE PROPOSED *P. MAXIMARTEZII* CYCLE.

Three-year reproductive cycle		Four-year reproductive cycle			
		1st year	2nd year	3rd year	4th year
Bud initiation	summer/fall	Bud initiation			1st year
Pollination	spring	Pollination			2nd year
Fertilization	summer	Fertilization			4th year
Seed dispersal	fall	Seed dispersal			4th year
<i>Pinus maximartinezii</i>					
Bud initiation	August/September				1st year
Pollination	May/June				2nd year
Fertilization	May/June				2nd or 3rd year (?)
Seed dispersal	October/November				4th year

Because of its thin bark and extremely slow growth, *P. maximartinezii* is especially susceptible to decimation by fire and human activities. Immediate conservation measures are needed to promote establishment and survival of natural regeneration on the site. Fire prevention and control must be top priorities while studies are conducted to assess the effect of cattle grazing on natural reproduction. A gene conservation project has been initiated by the CAMCORE Cooperative, North Carolina State University, USA, and the Centro de Genética Forestal, Chapingo, Mexico. A population-wide seed collection has been completed and ex-situ conservation plantings and research trials are planned at sites in Mexico and other countries.

ACKNOWLEDGMENTS

It is with sadness that I report that Carlos Mar Lopez, the second author of this paper, died in an accident in November, 1994. His dedication to the research and conservation of Mexican pines was outstanding and will be greatly missed.

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(Received 25 Feb 1994; revision accepted 16 Sep 1994)

A NEW SPECIES OF *QUERCUS*
(FAGACEAE, SECT. *LOBATAE*, GROUP *RACEMIFLORAE*)
FROM THE SIERRA MADRE OCCIDENTAL, MEXICO

R. SPELLENBERG AND J. R. BACON

Department of Biology, New Mexico State University,
Las Cruces, New Mexico 88003-0001, USA

D. E. BREEDLOVE

Department of Botany, California Academy of Sciences,
Golden Gate Park, San Francisco, CA 94118-4599, USA

ABSTRACT

The name *Quercus pennivenia* Trel. has been applied by many authors to an easily distinguished population of black oaks (*Quercus*, sect. *Lobatae*) from the group *Racemiflorae* that occurs in the northern Sierra Madre Occidental in northeastern Sinaloa, northwestern Durango, southeastern Sonora, and southwestern Chihuahua. The type of *Q. pennivenia* was collected south of this area and belongs to *Q. urbanii* Trel. sensu stricto. The northern population is herein named *Q. tarahumara* R. Spellenberg, J. Bacon & D. Breedlove, honoring the indigenous people whose lands this species inhabits. It is distinguished by its short and crowded pistillate inflorescences from *Q. urbanii* Trel. and *Q. radiata* Rose, both of which have long and uncrowded pistillate inflorescences. *Quercus tarahumara* usually also has denser glandular pubescence, and sparser stellate pubescence on the abaxial surface of the leaves.

RESUMEN

El nombre *Quercus pennivenia* Trel. ha sido usado por muchos autores como el nombre de una población fácilmente distinguida que localiza en el norte parte del Sierre Madre Occidental, en el noreste de Sinaloa, el noroeste de Durango, el sureste de Sonora, y el suroeste de Chihuahua. El tipo de *Q. pennivenia* fue colectado al sur de esta población y esta incluido en *Q. urbanii* Trel. sensu stricto. La población del norte esta descrito aqui como *Q. tarahumara* R. Spellenberg., J. Bacon & D. Breedlove, en referencia a las inflorescencias pistiladas breves y densas, que se sirve distinguir la especie nueva de *Q. urbanii* y *Q. radiata* Rose, ambos lo que tienen inflorescencias pistiladas largas y no compacta. *Quercus tarahumara* tambien usualmente tiene peloso glanduloso muy denso, y peloso estrellado mas disperso, en el envés de las hojas.

The genus *Quercus*, with 135–150 species occurring in Mexico (Nixon 1993a), is one of the most important genera of woody plants in the country, where it comprises a major component of the temperate woody vegetation (Rzedowski 1978). Spellenberg and Bacon determined nearly simultaneously and independently from Breedlove that a geographically discrete and morphologically recognizable series of populations of black oaks, section *Lobatae* (Nixon 1993b), in the group *Racemiflorae* (Trelease 1921, 1924), from the northern

Sierra Madre Occidental actually bears no name. These populations have been called *Q. pennevenia* Trel. by most workers (e.g., Brown 1982; Gentry 1942; Spellenberg 1992; Trelease 1924), a binomial based on a type that is best referred to *Q. urbanii* Trel. Trelease's concept of *Q. pennivenia* was confused, for the acorn clusters he illustrated for the species came from a very different black oak, *Q. mcvaughii* Spellenb. (Spellenberg 1992).

The type of *Q. pennivenia* is based on a collection made by B. Seemann in 1849, probably on the west slope of the Sierra Madre Occidental between Mazatlan and Durango (collected as *Q. crassifolia* Humb. & Bonpl. #1968). Seemann noted that the leaves were up to one foot across (Seemann 1856). He arrived in Durango at the end of December, 1849, found the flora in poor condition because of the cold, and decided to turn south rather than heading into Chihuahua as planned (Seemann 1856). Turner (1992) provides a map showing his approximate route. McVaugh (1972) estimates that his route from Mazatlan to Durango approximates the present highway Mexico 40. Our collections from the *Racemiflorae* from near Seemann's probable route between Mazatlan and Durango indicate that *Q. urbanii* (sensu stricto) occurs there, and not the northern taxon that we herein describe (collections cited in Appendix). Breedlove has seen the type and isotypes of *Q. pennivenia* at BM, GH, K, and Spellenberg has had fragments of leaves of all species of group *Racemiflorae* (*Q. conzattii* Trel., *Q. radiata* Trel., *Q. urbanii* Trel.) compared with the holotype. The type is vegetative and in its rather pale and moderately densely stellate and comparatively sparse glandular pubescence on the abaxial surfaces of the leaves is characteristic of *Q. urbanii* and compares well with leaf material collected from trees on the Mazatlan–Durango highway. These trees also have the long racemose pistillate inflorescences characteristic of *Q. urbanii*. Leaves of trees from the northern populations herein described as a new species have a sparse stellate tomentum on the abaxial surface that exposes the dense glandular hairs, which sometimes coalesce into brownish-golden irregular droplets, the abaxial surface golden brown rather than creamy-tan or tawny as in *Q. urbanii*. The northern populations also have very short and dense pistillate inflorescences. The population from the Sierra Surutato in Sinaloa is somewhat intermediate in leaf pubescence with *Q. urbanii* to the south, but has the dense pistillate inflorescences characteristic of the new taxon here described.

Even though Trelease indicated that this new member of the *Racemiflorae* occurred as far north as eastern Sonora and western Chihuahua, apparently only one collection was available to him at the time of his description of *Q. pennivenia*. In a survey of numerous herbaria in the United States, Mexico, and Europe (A, ARIZ, ASU, B, BR, CAS, CIIDIR, DAV, DS, F, G, GH, IBUG, IEB, K, LL, M,

MA, MEXU, MO, NMC, P, PH, TEX, UC, US) the earliest collection we note is that of C. V. Hartman in Sonora and Chihuahua, a collection made before 1900. Thus, it is possible that Trelease saw material of this new taxon from the region of the Sonoran–Chihuahuan boundary, but the type he selected is based on a collection from a northern population of *Q. urbanii*. The next oldest collection was made after Trelease's monumental review (1924) and is that of H. S. Gentry in 1936. Because *Q. pennevenia* is a synonym of *Q. urbanii*, we propose a new name for the distinct northern taxon that refers to the indigenous people whose homelands this oak inhabits.

Quercus tarahumara R. Spellenberg, J. Bacon, D. Breedlove, sp. nov. (Fig. 1).—TYPE: Mexico, Chihuahua, 1.25 km NW of Pinos Altos on descent into Las Baterias, elev. 2040 m, 28 Jun 1991, R. Spellenberg 10830 (holotype, NMC; isotypes, CAS, INIF, MEXU, NMC).

Arbores usque ad 3–12 altae; caules juniores dense pubescentes pilis aureis vel dilute brunneis; folia 9–25 cm longa 7–27 cm lata late obovata vel rotundata plerumque valde convexa, ad basim cordata, marginibus plus minusve integris vel 4–18 dentatis brevibus aristatis, folium omni venis 7–11 principalibus, epidermide abaxiali papillosa, plerumque dense pubescenti pilis glandulosis ochraceisque etiam sparsim pubescenti pilis stipitatis dilute brunneis, quoque pilo 3–6 ramoso contorto; inflorescentia pistillata 1–3 cm longa glandibus 2-ca. 16: cupulae plus minusve hemisphericae 5–7 mm longae 9–11 mm latae, squamis adpressis non incrassatis basaliter pubescentibus pilis pallidis adpressis; glandes annuae ovoideae dilute castaneae 8–14 mm longae 6–8 mm latae.

Trees 3–12 m tall, crown round. Trunk 1–3 dm diameter, bark dark gray to almost black, fissured and checkered on large trees. Branchlets 5–9 mm diameter in the first year, covered with tawny to golden-stellate tomentum, which becomes less dense and blackens in the second and third years; lenticels slightly raised, inconspicuous. Buds ovoid, 6–11 mm long, 3–5 mm wide, reddish-brown, the scales broadly ovate-acuminate, appressed pilose on abaxial surface. Leaves persistent into the second year, pendent. Stipules oblong or narrowly obovate, quickly deciduous, 6–15 mm long, 3–4 mm wide, membranous, ciliate on the margins, pilose abaxially. Petioles tomentose, 15–77 mm long, 2–5 mm thick. Leaf blades usually strongly convex, thick, stiffly leathery, olive-green and sublustrous adaxially, golden-brown abaxially with glandular and stellate hairs, broadly obovate to nearly round, 9–25 cm long, 7–27 cm wide, usually about as long as wide, gradually rounded in the apical half; apex rounded or obtuse, rarely short-acuminate; base broadly and shallowly cordate; margins thickened, revolute, standing well above the smaller veins on abaxial



FIG. 1. Holotype of *Quercus tarahumara* (NMC).

surface, subentire or with 4–18 low aristate teeth, the aristae 0–4 mm long; *veins* 7–11 on each side, ascending at 45–90° (wider angle in basal veins) from the midrib, the proximal branching and anastomosing well within the margin, the distal passing directly into teeth or aristae, occasionally branching and anastomosing with the margin; *adaxial surface* at first with golden glandular hairs that are soon deciduous, the mature surface hard, sublustrous, glabrous except for retention of stellate hairs near larger veins and especially near base of midvein, slightly rugose by the impression of the 1° and 2° veins, the veinlets in dried leaves slightly paler and level with the intervening areolae; *abaxial epidermis* minutely papillate, usually prominently golden-glandular with vermiciform hairs, and more or less stellate pubescent, the vermiciform glandular hairs hiding up to 50% of the epidermis, sometimes apparently coalescing into brownish glandular droplets, and with sparse stipitate 3–6-branched hairs, the contorted branches intertwangled and not obscuring the epidermis; *veins on abaxial surface* elevated, conspicuous, the 4° and smaller veinlets conspicuous and appearing paler against the background, not obscured by the stellate tomentum. *Staminate aments* 6–14 cm long; rachis sparsely villous, loosely flowered; pedicels 0–ca. 2 mm long; perianth tan, campanulate, glabrous except for the ciliate margin and a thick tuft of hairs near the base of the filaments; stamens 7–11; anthers 1.5–2 mm long, glabrous, prominently apiculate. *Pistillate inflorescences* 1–3 cm long, dense, raceme- or spike-like, with 2–ca. 16 sessile or subsessile flowers (Fig. 2). *Fruit* annual crowded in a spike-like inflorescence up to 3 cm long, ca. 2 cm wide; *cup* 9–11 mm wide, 5–7 mm long, ± hemispheric; scales reddish-brown, thin, appressed pubescent to ± glabrate, the pubescence commonly much denser near the apex; apices thin, rounded, appressed; *acorn* ovoid, 8–14 mm long, 6–8 mm in diameter, pale brown, ca. 30% included in the cup.

Common names for *Quercus tarahumara* in the region are “gueja” or “cusi gueja de la sombrilla.” On one of Gentry’s specimens from Sinaloa a common name “encino cacachilla” is recorded.

Quercus tarahumara has rarely been collected in flower, a fact probably contributing to its lack of earlier recognition. The few such collections indicate a flowering period from December to June. The species occurs from 1020–2200 m on igneous and presumably acid, more or less sterile reddish or pale gray epithermically or hydrothermally altered substrate, or on benches of white ashy soil not dramatically altered, along the west slope of the Sierra Madre Occidental. It extends from Municipio Temosachi in west-central Chihuahua and Municipio Yecora in adjacent east-central Sonora southward to Municipio Badiraguato in northeastern Sinaloa and Municipio Tepehuanes in northwestern Durango. *Quercus tarahumara* commonly occurs as islands among *Q. albocincta* Trel., *Q. arizonica*



FIG. 2. Variation in pistillate inflorescences in the type population of *Quercus tarahumara*: (left) fruiting clusters of holotype (NMC); (right) fruiting clusters of isotype (NMC).

Sarg., *Q. chihuahuensis* Trel., *Q. coccobifolia* Trel., *Q. hypoleucoides* Camus, *Q. mcvaughii* Spellenb., *Q. oblongifolia* Torr., *Q. toumeyi* Sarg., and *Q. viminea* Trel. At one known locality where it occurs at its lower elevational range, Santa Rosa, Sonora, it is surrounded by dry tropical forest.

ACKNOWLEDGMENTS

We thank the curators of the herbaria cited for making material available for our study. Fred Barrie kindly compared leaf fragments from several collections of group *Racemiflorae* with the type of *Q. urbanii* at BM for Spellenberg. Guy Nesom assisted with the Latin description. Paul Martin provided information about habitat and common names of the new species.

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(Received 5 Apr 1994; revision accepted 16 Aug 1994)

APPENDIX

Specimens of *Q. urbanii* and *Q. tarahumara* examined, all from Mexico. Collections within each state are arranged alphabetically by collector.

Specimens of *Quercus urbanii* Examined

GUERRERO/MICHOACAN: *Langlasse* 1066, Sierra Madre, 1800 m, 20 VI 1899, (US). SINALOA: *Breedlove* 44915, Mpio Concordia, near Loberas microwave station, 4 Aug 1980, (CAS); *Breedlove* 58844, 18 Oct 1963 (CAS); *Cavagnaro* 441, Highway 40 9 mi SW of El Palmito, 4 Dec 1983, (MEXU); *Spellenberg and Bacon* 11775, Mpio. Concordia, Hwy. 40, 16 km SW of Durango state line, SW edge of Loberas, 27 Jan 1993, (CAS, CIIDIR, MEXU, NMC, NY). WITHOUT STATE CITED: *Seemann* 1968, Sierra Madre (BM [photocopy NMC], GH, K).

Specimens of *Q. tarahumara* Examined

CHIHUAHUA: *Allred* 5403, Puerto Gallego, 12 km SE of Cerocahui at Arroyo de las Herraduras, 12 Jun 1991, 2140 m (NMC, NMCR); 5425, Cascada Wicochi canyon E of Cerocahui, 1640 m, 13 Jun 1991 (NMC, NMCR); *Breedlove* 61201, 61205, 61206, 10 km E of Maycoba, 1590 m, 29 Aug 1984 (CAS); 61208, 61213, 61214, 29 km E of Yepachic along road to Chihuahua, 1980 m, 29 Aug 1984 (CAS); *Gentry* 8051, Rancho Byerly, Sierra Charuco, 17–25 Apr 1948 (ARIZ, MEXU, RSA), 8051a (RSA); *Hartman* 1024, near Batopilas (without date) (GH, MO, UC, US); *Hewitt* 264, Cerro Colorado, San Gabriel Mine, 22 March 1948 (GH); *Holm* s.n., km 38 between Ocampo and Moris, 1700 m, 25 Jun 1987 (ARIZ); *Knobloch* 455, La Bufa on Rio Batopilas, 13 Sep 1975 (CAS); *Langille* 10, Rancho Byerly, Sierra Charuco, summer 1946 (RSA); *Moore et al.* 247, 248, Mpio. Ocampo, roadside near Ocampo near km 35, 24 Jun 1986 (NMC); 260, Ocampo mine site, just S of Ocampo, 26 Jun 1986 (NMC); *Spellenberg* 10830, 1.25 km NW of Pinos Altos on descent into Las Baterias, 2040 m, 28 Jun 1991 (CAS, INIF, MEXU, NMC); *Spellenberg, Boecklen and Zimmerman* 9830, 15 air km NNE of Ocampo at Pinos Altos, 2100 m, 22 Jun 1989 (CAS, MEXU, NMC, NY, TEX); 9834, 24 km NW of junction to Ocampo on road between Basaseachic and Yecora, 1950 m, 21 Jun 1989 (CAS, MEXU, NMC);

9840, 27 km W of junction of road to Ocampo with Basaseachic–Yepachic road, 1800 m, 22 Jun 1989 (MEXU, NMC); 9847, 6 km W of Yepachic, 18 km E of Sonoran border on Basaseachic–Yecora road, 1890 m, 22 Jun 1993 (MEXU, NMC); 9854, 5.5 km E of the Chihuahua–Sonora border on road between Yepachic and Maycoba, 1585 m, 23 Jun 1989 (CIIDIR, MEXU, NMC); Spellenberg, Corral, Lebgue and Mahrt 10066, Mpio. Ocampo, Parque Nacional de Cascada Basaseachic, 1700 m, 11 Nov 1989 (Esc. Sup. Agric. "Hermanos Escobar," Univ. Auto. Chih., NMC); Spellenberg and Jewell 9382, Mpio. Moris, 6 mi W of Ocampo on the road to Moris, 1950 m, 13 Sep 1987 (CAS, Esc. Sup. Agric. "Hermanos Escobar," INIF, MEXU, NMC); 9389, Mpio. Moris, 15 road mi W of Moris, 1524 m, 14 Sep 1987 (CIIDIR, NMC); Spellenberg et al. 8106, ca. 25 air mi SW of San Juanito, Maguarichi, 1 mi E of village, 28 Apr 1985 (BH, MEXU, NMC, NY); T R and R K Van Devender and P S Martin 87-202, 6 km WNW of Ocampo on road to baseball field, 1829 m, 25 Jun 1987 (NMC). DURANGO: Benitez 510, Mpio. Tepehuanes, 3 km de la Mango, 2210 m, 26 Apr 1989 (CIIDIR); Luquin, Santana y Oruelas 267, Mpio. Tepehuanes, comunidad de Boca de Sta. Catarina, "Frailecillos," 2400 m, 26 Oct 1989 (CIIDIR). SINALOA: Breedlove 16512, 5 mi W of Santa Rita E of the Los Hornos to Surutato Road, Sierra Surutato, 1982 m, 24 Feb 1969 (CAS, RSA); 19227, Sierra Surutato, Mpio. Badiraguato, N side of Bufa de Surutato, 2195 m, 8 Mar 1971 (CAS); Breedlove and Kawahara 16829, Mpio. Badiriguato, Sierra Surutato, 0.5 mi N of Los Oruros, 1 Nov 1969 (CAS); Breedlove and Thorne 18360, Mpio. Badiriguato, Sierra Surutato, e mi N of Los Ornos along road to Ocurahui, 1982 m, 2 Oct 1970 (CAS, RSA); Castro 2222, Choix, Nov 1951 (MEXU); Gentry 1983, Rio Mayo, Tepopa, 4 Apr 1936 (MEXU); 6184, Ocurahui, Sa. Surutato, 2134 m, 27 Aug 1941, (ARIZ, CAS); Kimnach and Sanchez-Mejorada 2085 (MEXU), 2087 (US), 22 mi past Tasajera on road to San Vicente, 1463 m, 8 Nov 1977; Vega 2568 Mpio. Badiriguato, alrededores de Surutato, 1700 m, 11 Dec 1987 (IBUG, IEB, MEXU). SONORA: Breedlove 61116, 61123, 61124, 61125, 61126, 8 km SE of Trigo on road from Yecora to Sahuaripa, 1370 m (CAS); Gentry 2226, Rio Mayo, Tepopa, 1524 m, 4 Jun 1936 (A, ARIZ, CAS, K, MEXU, MO, UC, US); Hartman 343, Sierra del Nacori, 15 Dec 1890 (GH, K US); Hernandez M. 2383, La Joya, Taimuco, Alamos near border with Chihuahua, 10 Jun 1976 (MEXU); Jenkins and Martin 88-247, 3 km W of Las Chinacas at Cerro las Tinajas, 1400 m, 13 Oct 1988 (ARIZ); Jenkins & Todd 93-43, Mpio. de Alamos, NE of Alamos, E side of Cerro Agujudo, near Rancho Santa Barbara, 29 May 1993 (NMC); Marshall 182, Sa. Saguaribo, San Antonio, se Sonora, 1524 m, 28 July 1961 (ARIZ); Martin and O'Rourke s.n., Santa Rosa (Yaqui River drainage), 1 km SSW of town, 1020 m, 11 May 1987 (ARIZ); Pennell 19588, Cerro Saquarivo, E of San Bernardo, 7 Aug 1935 (PH, US); Spellenberg, Boecklen and Zimmerman 9866, 9868, 4.5 km W of the Chihuahua–Sonora boundary on road between Yepachic and Maycoba, 1430 m, 23 Jun 1989 (MEXU, NMC); 9873, 13 km E of Yecora on road to Maycoba, 1460 m, 23 Jun 1989 (NMC); Turner and Martin 79-352, 2.5 mi by road S of Huicoche, 1540 m, 6 Oct 1979 (ARIZ).

SESSILE-FLOWERED SPECIES IN THE
NAVARRETIA LEUCOCEPHALA GROUP
(POLEMONIACEAE)

ALVA G. DAY

Department of Botany, California Academy of Sciences,
Golden Gate Park, San Francisco, CA 94118

ABSTRACT

Navarretia myersii and *N. prostrata* of sect. *Navarretia* have a reduced habit, are nearly acaulescent, and have a terminal inflorescence. Mature floral heads bear sessile flowers and bracts on a common receptacle, surrounded by involucral leaves and bracts. This combination of features occurs also in a related, but new and rare plant described here as *N. myersii* subsp. *deminuta*. The three taxa are members of the *N. leucocephala* group, all of which are restricted to vernal pool habitats.

Members of the *Navarretia leucocephala* group of sect. *Navarretia* (Polemoniaceae) are all adapted to a vernal pool habitat. Included are *N. involucrata* Ruiz & Pavon of Argentina and Chile, which is the type species of the genus (Grant 1959), and four North American species, as recently treated (Day 1993a). These are *N. leucocephala* Benth. (with five subspecies), *N. fossalis* Moran, *N. prostrata* (A. Gray) E. Greene and *N. myersii* P. S. Allen & A. G. Day. The last two species differ from the others in having a reduced habit and involucrate inflorescence. A related, and newly discovered taxon is described below as *N. myersii* subsp. *deminuta*.

The first collection of *N. myersii* subsp. *deminuta* was brought to me as an unidentified *Navarretia* by Linda Huntington and Margaret Rockwood, who were making a botanical survey of property in southern Lake County, California (Huntington & Rockwood 1992). The plants were similar to *N. myersii*, a rare species that was described recently (Day 1993b).

***Navarretia myersii* P. S. Allen & A. Day subsp. *deminuta* A. G. Day, subsp. nov. (Fig. 1).**—TYPE: USA, California, Lake County, 2 m. SE of Middletown, Long Valley, Butts Canyon Rd. at jct. with Callayomi Rd., 2 May 1994, Day 94-1 (Holotype, CAS, Isotypes RSA, US).

Affinis subsp. *myersii* sed differt a foliibus brevibus (1–5 cm longibus); lobi bractearum multi et multipartiti cum dentibus attenuatis; corolla azurea, tubus corollae brevis, calyce 1–1.2 plo longior.

Plants generally in dense colonies, acaulescent or nearly so, hypocotyle thickened. Basal stem internodes 0–10 mm long. Leaves 2–

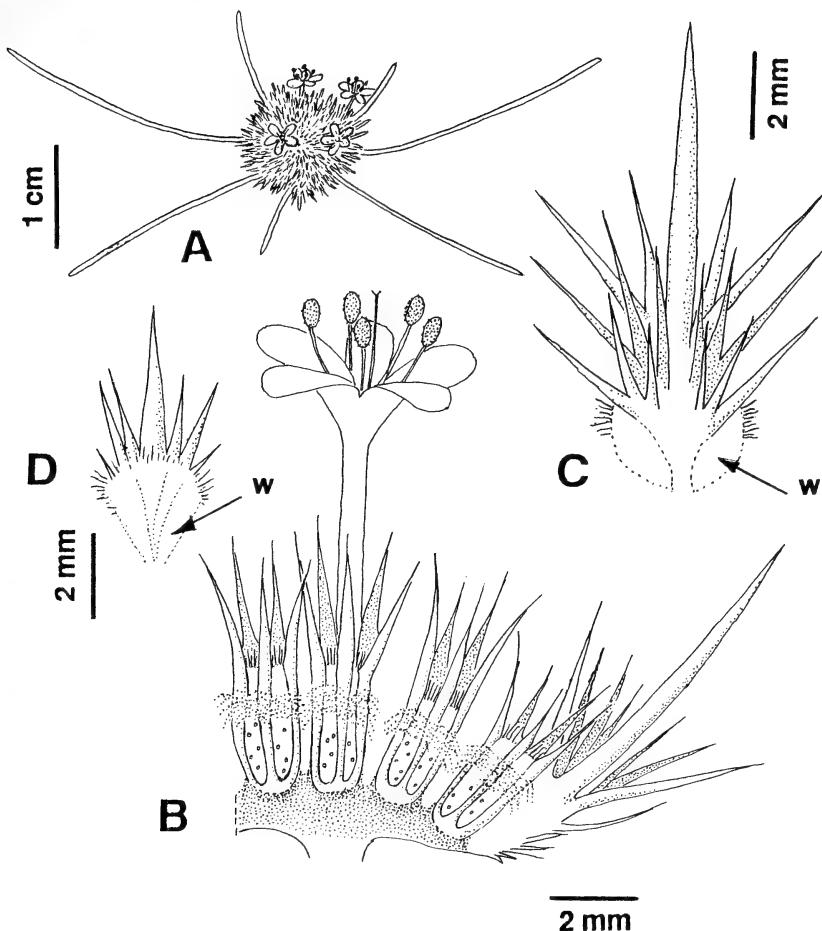


FIG. 1. *Navarretia myersii* subsp. *deminuta* A. G. Day, subsp. nov. A. Habit of plant, top view. B. Segment of inflorescence showing four flowers, one in bloom at anthesis. For clarity only one bract is shown (far right). Stippled area = receptacle. C-D. Bracts. w = membranous wing. C. Outer bract (dorsal view). D. Inner bract (ventral view). A. Drawn from Huntington & Rockwood 10 (CAS). B-D. Drawn from fresh specimens (Day 94-1 CAS). Drawings by author.

4 in opposite pairs, linear, entire, 1–5 cm long, radiating from beneath head, usually much exceeding it. Head 8–20 mm dia., terminal and involucrate with spreading, fleshy receptacle. Involucral bracts and flowers sessile on the common receptacle. Outer bracts 3–5, 1–2 cm long, winged and dorsally lobed at base; wing membranous, slightly villous, lobes numerous, attenuate, glabrous, spreading, forked or with 4–5 attenuate teeth. Inner bracts shorter, equaling or slightly

TABLE 1. COMPARISON OF THE INVOLUCRATE SPECIES OF *NAVARRETIA*.

	<i>N. myersii</i> subsp. <i>myersii</i>	<i>N. myersii</i> subsp. <i>deminuta</i>	<i>N. prostrata</i>
1. No. of secondary floral branches	0 (0–2)	0 (0–2)	Many (1–20)
2. Leaf form	Entire, or lobed only near base	Entire, or lobed only near base	Lobed from base to apex
3. Outer bract dissection	Lobes few, none above middle	Lobes many near base, few or none above	Lobed from base to apex
4. Bract wing	Densely villous	Slightly villous	Slightly villous
5. Calyx lobe length	< tube	= tube	< tube
6. Corolla length	17–21 mm	12–13 mm	6–9 mm
7. Corolla tube	2–4 × calyx	1–1.2 × calyx	< 1–1 × calyx
8. Corolla color	White	Blue	White or blue
9. Pollen color	Yellow	White	White
10. No. of seeds per capsule	4–6	4–6	5–25

exceeding calyx. Calyx 5–6 mm long, villous about middle, lobes subequal tube, entire, attenuate, spreading. Corolla blue, 12–13 mm long, tube 7–8 mm long, exceeding longest calyx lobe by 1–2 mm. Stamens exserted, equaling corolla lobes. Pollen white. Style exserted to anther level, stigmas minute. Seeds 4–6 per capsule. Clay-loam soil of vernal pools and roadside depressions. A rare endemic, known only from type locality where it is abundant and well-established. Flowering April–May.

Paratypes: USA, California, Lake Co., Long Valley, at the type locality 2 m. E of Middletown, SW side Butts Crn. Road at intersection with Callayomi Rd., 21 May 1992, Rockwood & Huntington 10 (CAS); (same locality) 5 May 1993, Rockwood & Huntington 41 (CAS); 14 May 1994, Spencer 4514-H1 (RSA).

This new *Navarretia* is potentially endangered by its occurrence on a forty-acre parcel that is likely to be subdivided and sold, with probable disturbance of the vernal pool habitat.

The name *deminuta* refers to the small size of the plants, but other differences that distinguish it from subsp. *myersii* and *N. prostrata* are shown in Table 1. Compared with subsp. *myersii* it differs especially in the abundance of attenuate bract lobes at the base of the head, the blue (not white) corolla, and the much shorter corolla tube.

Observations and collections of *N. myersii* subsp. *deminuta* in three successive seasons, 1992–1994, showed how it responded to two relatively dry years and one wet year (spring 1993). The plants had the same basic morphology in the wet year as in the dry years, differing only in that the 1993 plants had longer leaves and generally broader heads with more numerous flowers.

Subspecies *deminuta* is isolated geographically from subsp. *myersii*, the latter occurring in a few rare localities bordering the Sierra Nevada foothills in California's Central Valley (Day 1993a, b) and from *N. prostrata*, which is mostly in Southern California, with a few sites in Monterey County and western central California.

Because subsp. *deminuta* appears somewhat different from subsp. *myersii* its status as possibly a distinct species was considered. However, there are intermediates between the two taxa. These include collections of *N. myersii* that were cited earlier as paratypes (Day 1993b). These specimens are less extreme than the type of subsp. *myersii*, and except for their white corollas they are very similar to subsp. *deminuta*. Thus, specimens from Amador Co. (Heller 16114, UC) and from Sacramento County (Day & Allen 88-10, CAS) have shorter corolla tubes than those from the type locality. Also, bracts of the Sacramento County plants usually have more lobes than those of the type material.

The cited intermediate collections from Amador and Sacramento counties are from considerably north of the type locality of *N. myersii* (E Merced County), but far southeast of the type locality of subsp. *deminuta*, and are thus geographically intermediate as well.

The inclusion of the Lake County race of *N. myersii* as a subspecies of *N. myersii* results in a range extension from the eastern side of the Central Valley to the Coast Ranges of southern Lake County, California.

SPECIES COMPARISONS

In most Polemoniaceae branching is cymose (Grant 1959). This is true of *Navarretia*, but because the inflorescence is a head, the branches and pedicels are much reduced. Flowers of *N. leucocephala* and *N. fossalis* are short-pedicellate to sessile, but on closer examination they appear grouped in several clusters due to branching at a lower level within the head.

The modified inflorescence type of *N. myersii* and *N. prostrata* appears as a telescoped version of this pattern, and exhibits probably the greatest extreme of reduction in the *N. leucocephala* group. With basal stem internodes foreshortened, the leaves and outer bracts radiate outward in a whorl beneath the head (Fig. 1A). The mature inflorescence is terminal and unbranched, consisting of sessile flowers and associated sessile bracts on a common receptacle (Fig. 1B). Observed at a young stage the flowers arise in cymose sequence from the receptacle in the axils of bracts, but complete their development at one level (Fig. 1B).

The central head expands in diameter as new flowers arise in the axils of peripheral or inner bracts. As many as sixty flowers at various

stages of maturity were counted in a single head of *N. myersii* subsp. *myersii* (Day 1993b).

Secondary floral branches are rarely found in the subspecies of *N. myersii*, and are at most only one or two. A vigorous plant of *N. prostrata*, however, may have numerous secondary branches spreading from beneath the central head, as pictured by Mason (1951, p. 444).

Further comparisons of these two species (Table 1) shows that they differ also in leaf lobing (no. 3) and in the number of seeds per capsule (no. 10). In these two characters *N. prostrata* is more like *N. fossalis* than it is like *N. myersii*. However, differences between *N. prostrata* and *N. fossalis* are numerous, and are maintained in nature. The two species occur sympatrically on the Santa Rosa Plateau in Riverside County where they show no intergradation (Day 1993b). This was also verified recently by Spencer (personal communication, Spencer 4601-11, 4601-12, RSA).

Navarretia myersii and *N. prostrata* are placed together in the key below on the basis of their similar reduced habit and villous calyx tube. This may reflect relationship, due to a shared monophyletic origin, or, alternatively, the reduced inflorescence habit may have arisen more than once in different, but related species.

KEY TO THE *NAVARRETIA LEUCOCEPHALA* GROUP, AND TO THE INVOLUCRATE SPECIES

1. Head cymosely branched within; flowers pedicellate to sessile; flowers and bracts borne separately; calyx tube generally not villous except in *N. fossalis* *N. leucocephala* and *N. fossalis*
- 1'. Head unbranched within, except secondary floral branches sometimes present: flowers and bracts sessile on a common receptacle; calyx tube villous.
 2. Corolla 6–9 mm long; calyx lobes often 3-fid; leaves strap-shaped, lobed from base to apex; secondary floral branches frequent (1–20) *N. prostrata*
 - 2'. Corolla 12–21 mm long; calyx lobes entire, rarely 2- or 3-fid; leaves linear and entire, or lobed near base; secondary floral branches rare (0–2) *N. myersii*
 3. Corolla blue, tube 1–1.2 × calyx; outer bracts at base of head many-lobed, bract wings slightly villous subsp. *deminuta*
 - 3'. Corolla white, tube 2–4 × calyx; outer bracts at base of head few-lobed, bract wings densely villous subsp. *myersii*

ACKNOWLEDGMENTS

I thank Linda Esposito (=Huntington) and Margaret Rockwell for finding and sharing the new *Navarretia*, as well as for their unpublished survey, which provided much useful information. Thanks are due to Stanley Spencer (RSA) for shared observations from his *Navarretia* research and field work. Suggestions by Frank Almeda and John Strother concerning the manuscript are much appreciated. Diana Lusk edited the Latin diagnosis. Access to the property where the new *Navarretia* occurs was possible due to the interest and cooperation of the owner, Dr. Olaf Larson. I appreciate the courtesies extended by curators of the following herbaria: CAS, DS, JEPS, RSA, UC, and US.

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(Received 2 Jun 1994; revision accepted 7 Oct 1994)

ANNOUNCEMENT

URGENT CALL FOR CORRECTIONS TO THE JEPSON MANUAL

Have you found any typographical errors or minor substantive errors in The Jepson Manual: Higher Plants of California (J. Hickman, ed.)? If so, the Jepson editors would be grateful to receive your input before April 1, 1995 to aid in production of the next printing of The Jepson Manual (1st edition). Corrections that change pagination cannot be considered for incorporation in the next printing (but see below). Any substantive corrections that require editorial judgement should be accompanied with documentation (e. g., literature or voucher citation). Please send your corrections to Bruce Baldwin, Curator of the Jepson Herbarium, 1001 Valley Life Sciences Bldg. #2465, University of California, Berkeley, CA 94720-2465. e-mail communication of your corrections can be sent to: jepson@ucjeps.berkeley.edu. Thank you!!

In preparation for production of a more extensively revised 2nd edition of The Jepson Manual, the Jepson editors would also appreciate any documented corrections of more substantial errors or problems in the Manual. All corrections that would change pagination of the Manual fall under this category. To aid editorial procedures, please segregate any corrections of this type under separate heading from typographical and other minor corrections discussed in the previous paragraph. These corrections can be sent to the same address given above.

GAP ANALYSIS OF THE ACTUAL VEGETATION OF CALIFORNIA 1. THE SOUTHWESTERN REGION

FRANK W. DAVIS

Center for Remote Sensing and Environmental Optics, and
Department of Geography, University of California,
Santa Barbara, CA 93106

PETER A. STINE

National Biological Service, Sacramento, CA 95814

DAVID M. STOMS

Center for Remote Sensing and Environmental Optics, and
Department of Geography, University of California,
Santa Barbara, CA 93106

MARK I. BORCHERT

Los Padres National Forest, Goleta, CA 93117

ALLAN D. HOLLANDER

Center for Remote Sensing and Environmental Optics, and
Department of Geography, University of California,
Santa Barbara, CA 93106

ABSTRACT

Gap Analysis is a method of conservation risk assessment that evaluates the protection status of plant communities, animal species and vertebrate species richness by overlay of biological distribution data on a map of existing biological reserves. The National Biological Service has undertaken a national Gap Analysis that is being conducted by individual states but that will eventually produce regional and national assessments. Given California's size and complexity, we are conducting separate Gap Analyses for each of the state's 10 ecological regions, as delineated in *The Jepson Manual*. Here we summarize our findings on the distribution of plant communities and dominant plant species in the Southwestern Region of California, exclusive of the Channel Islands. We tabulate and discuss regional distribution patterns, management status and patterns of land ownership for 76 dominant woody species and 62 natural communities. Nineteen of 62 mapped communities appear to be at risk, as determined by their poor representation in existing reserves, parks or wilderness areas. Communities restricted largely to the lower elevations, such as non-native grasslands and coastal sage scrub types, are clearly at considerable risk. A majority of the lands at these elevations have already been converted to agricultural or urban uses and most of the remaining lands are threatened with future urbanization. Areas that appear to be of highest priority for conservation action based on agreement between our analysis and a recent assessment by The Nature Conservancy include the Santa Margarita River, San Mateo Creek, Miramar Mesa, Santa Clara floodplain near Fillmore, Sespe and Piru Canyons, and Tejon Pass.

California's flora includes over 5800 native vascular plant species, or roughly 25% of the flora of the continental U.S. (Mooney 1988; Hickman 1993). One thousand four hundred and sixteen species (24.2%) and 737 subspecies or varieties are endemic to the state. During the past century this remarkable native flora has been seriously diminished by agricultural, residential and industrial development and by the spread of naturalized, alien plant species. Six hundred plant taxa and 200 natural communities are now considered endangered or threatened with extinction, and some 200 natural plant communities have been significantly reduced from their original distribution (Jones and Stokes Associates 1987; Jensen et al. 1990).

Considerable resources have been invested in conserving California's biodiversity on both public and private lands, which account for 51.5% and 48.5% of the state, respectively. Most efforts focus on single species or site specific issues, particularly in response to federal and state endangered species legislation. This piecemeal approach to conserving California's flora cannot possibly succeed, first because the economic cost is ultimately higher than the public is willing to bear, and secondly because of the inevitable fragmentation and cumulative degradation of habitats that accompanies localized impact mitigation schemes.

Most conservation biologists agree that the best strategy for conserving biodiversity is to maintain native species in extensive, natural landscapes that are sufficiently linked to allow interaction and genetic interchange among disjunct populations (Noss 1983). This requires a cohesive, representative system of areas managed for the maintenance of native biodiversity. (We avoid using the term "reserve" or "sanctuary" because management for maintenance of biodiversity does not necessarily preclude multiple-use land management strategies.) To implement such a system requires knowledge over regional to statewide extent of ecosystem patterns and dynamics, as well as species distributional status and trends, phylogeny, life history, and habitat requirements. It also requires more detailed, local information on population dynamics and genetics, as well as socioeconomic and political information. The broader-scale ecosystem assessment is sometimes referred to as the "coarse filter" approach to conservation planning, as opposed to the "fine filter" studies of individual species and localities.

In an effort to provide a coarse-filter perspective on biological diversity and its current conservation status, the National Biological Service is coordinating a national Gap Analysis program. The term "Gap Analysis" refers to the evaluation of the protection status of plant communities and terrestrial vertebrates by overlay of biological distribution data on a map of existing biological reserves using a geographic information system (GIS) (Scott et al. 1993). We are

conducting a Gap Analysis of California with cooperation and collaboration from dozens of public and private organizations (see Acknowledgements). The analysis requires preparing a statewide map of actual vegetation, supplemented with more detailed locality data for plant taxa of special concern. Given the physiographic and biological complexity of California, we are conducting separate analyses for each of the state's geographical regions, as delineated in *The Jepson Manual* (Hickman 1993). Our hope is that this information will help to provide a regional context for more detailed, local investigations. Our intent is also to assist botanists, ecologists, and natural resource analysts in prioritizing community types and geographical areas for immediate, more detailed conservation assessments and actions.

This paper summarizes our findings on the distribution of plant communities and dominant plant species in the Southwestern Region of California, exclusive of the Channel Islands (Fig. 1). We describe the development of the database and illustrate its application to biogeographic research and conservation assessments. Dominant woody species and plant communities are tabulated in terms of regional distribution patterns, management status and patterns of land ownership. We test the hypothesis that land ownership and management status can be used to identify plant communities at high risk of becoming threatened or endangered, and find strong support for the assertion. Based on criteria that we develop to identify at-risk communities and species, we identify a number of widespread, upland plant communities and dominant species that we believe deserve more attention in conservation planning efforts. Finally, we combine maps of communities-at-risk with information from the Natural Diversity Data Base (NDDB) and The Nature Conservancy of California to locate and highlight areas that emerge as high priority for conservation planning and management.

STUDY AREA

Geography. The Southwestern Region includes 3,383,160 ha, roughly 8 percent of California. It lies within the California Floristic Province and is divided into four subregions and six districts (Fig. 1). Subregions include the South Coast, Channel Islands, Transverse Ranges and Peninsular Ranges. Districts of the Transverse Ranges include the San Bernardino Mountains, San Gabriel Mountains, and Western Transverse Ranges. The San Jacinto Mountains are considered a separate district of the Peninsular Ranges.

The region is bounded by the Sonoran Desert and Mojave Desert regions on the east and the crest of the Santa Ynez Mountains and the upper Cuyama Valley on the north. The boundary at the southern

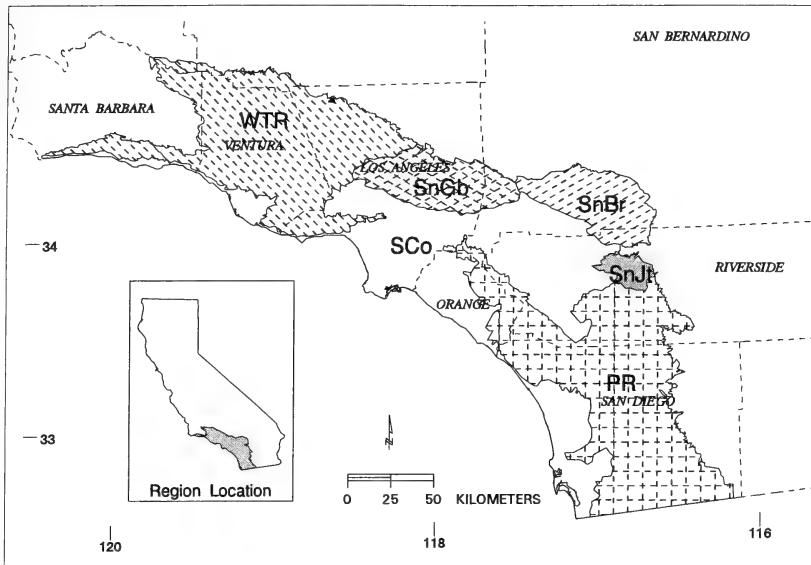


FIG. 1. Location map and geographic subregions of Southwest California defined on the basis of topography, climate, and plant community variation (Hickman 1993). We revised the northern boundary of the region, placing the upper Santa Ynez River basin and southern Sierra Madre Ranges in the Central Western Region. Subregions include the Transverse Ranges, which are further subdivided into the Western Transverse Ranges (WTR), San Gabriel Mountains (SnGb), San Bernardino Mountains (SnBr) and San Jacinto Mountains (SnJt), Peninsular Ranges (PR), and South Coast (SCo).

end of the region is defined as the Mexican border, although vegetation similar to that found in southwest San Diego County extends south into Baja California for roughly 300 km, where there is an abrupt transition to a more arid adapted flora (Westman 1981).

Based on 1990 census data, 16,539,858 people (56% of California's total population) reside in the region. This region has experienced extraordinarily rapid population growth in recent decades. From 1980 to 1990, the population of San Bernardino and Riverside counties grew at a rate of more than 50%, San Diego County grew at a rate of 30–40%, Orange and Ventura counties expanded by 20–30%, and Santa Barbara and Los Angeles counties grew 5–20% (Goodenough 1992). The population of some localities such as Vista and San Marcos in San Diego County grew by more than 100% over this period (Griffin 1992).

Physiography and geology. Forty-six percent of the region is lower than 500 m above mean sea level. Only 3.5% of the region is above 2000 m, and <0.1% is above 3000 m. The southern half of the

region is dominated by the Peninsular Ranges. The northern portion of the region is part of the complex Transverse Ranges province. At least five main mountain ranges comprise the Peninsular Ranges of southern California: the San Jacinto Range (summit elevation 3325 m), the Santa Rosa Range (2680 m); the Santa Ana Mountains (1755 m); the Agua Tibia Mountains (1880 m) and the Laguna Mountains (1940 m). The basement rock of the Peninsular Ranges is a granitic batholith, consisting mainly of quartz diorite dating from the lower Cretaceous period (Norris and Webb 1990). Some older roof pendants remain, particularly in the western region, consisting of altered schist and gneiss, with some limestone. Major fault valleys include the Elsinore fault zone and the San Jacinto fault zone.

The major mountain ranges of the Transverse Range include the Santa Ynez Mountains (1325 m), the Topatopa Range (2060 m), the Santa Monica Mountains (925 m), the San Gabriel Mountains (3080 m) and the San Bernardino Mountains (3385 m). The San Gabriel and San Bernardino are mainly granitic and metamorphic rocks from the lower Cretaceous. The Santa Monica Mountains are comprised largely of Miocene marine sedimentary rocks and volcanic rocks, whereas the Santa Ynez and Topatopa mountains are predominantly Eocene interbedded marine sandstones and shales.

Climate. There is a strong climatic gradient from low coastal areas to high elevations of the interior, and a secondary gradient from north to south (Bailey 1966). Mean temperatures along the coast range from around 5°C in winter to 10°C in the summer. In contrast, mid-elevations further east range from 2°C in winter to 22°C in summer. Annual precipitation averages 250–500 mm at lower elevations to greater than 1500 mm at high elevations in the Transverse Ranges. Total annual precipitation at coastal localities decreases from 400 mm in the north to 250 mm at San Diego. However, southern areas receive more summer precipitation associated with tropical hurricanes. Annual moisture balance ranges from a surplus of 100–200 mm in the mountains to deficits of 200–600 mm at lower elevations. Within the region, topography and variable coastal influence combine to produce at least 5 general climatic types, including warm steppe, warm mediterranean, cool mediterranean, maritime mediterranean and microthermal (montane).

Soils and vegetation. Soil patterns are very complex, reflecting interactions among geology, topography, climate, geomorphology and vegetation. In general, mollisols predominate in the interior faulted valleys, while a diverse group of alfisols occur on the terraced coastal sediments. The mountain soils are not well characterized, but are likely to be comprised of poorly developed, excessively drained entisols. The California Natural Diversity Data Base (NDDB) system currently recognizes 272 natural communities occurring in the

state (Holland 1986). Of these, 89 (33%) occur within the Southwestern Region. A list of 87 widespread trees and shrubs that are frequent canopy dominants in upland vegetation of the region are provided in Appendix A. Appendix B lists 73 communities that we have mapped, as well as 11 other community types described by Holland.

Upland natural areas of this region are dominated by 24 major terrestrial community types. Annual grasslands, woodlands and soft chaparral communities dominate lower elevations, giving way to hard chaparral at mid-elevations, and then to mixed evergreen forest and mixed conifer forest at the highest elevations. Slopes adjacent to the Mojave and Sonoran Deserts support drier shrubland types, as well as pinyon and juniper woodlands.

Taxa of special concern. NDDB lists 93 plant species, 28 subspecies, 26 plant varieties, and 34 terrestrial plant communities of special concern within the region. As of 1990, 4255/18,937 (25.5%) of all NDDB records fell within this area. High concentrations of threatened and endangered species occur near the coast in western San Diego County (Imperial Beach, Otay Mesa, Del Mar quads), near Cuyamaca Peak, in the Lake Mathews Basin, and near Big Bear Lake in the San Bernardino Mountains.

Land ownership. Sixty percent of the land area is in private ownership, much of it at lower elevations and already converted to urban or agricultural uses. Only a small fraction of private land is managed for biodiversity protection, including The Nature Conservancy preserves and Audubon Society sanctuaries. The steeper, montane areas are largely managed by public agencies such as the U.S. Forest Service (29% of the region), Bureau of Land Management (3%), Department of Defense (2%), and the California Department of Parks and Recreation (2%). Lands owned and managed by Native Americans cover only 2% of the region, mainly in San Diego County.

Four National Forests (from south to north, the Cleveland, San Bernardino, Angeles, and Los Padres) are managed primarily for watershed conservation, recreation, and fire protection. Congress passed legislation in 1964, 1968, 1984, and 1992 designating twelve wilderness areas on these National Forests. Similarly, California Parks and Recreation has designated four wilderness areas that lie wholly or partially within the region. The National Park Service, State Parks, and private conservancy groups are actively purchasing land in the Santa Monica Mountains National Recreation Area to preserve the area for recreational and natural values.

METHODS

Vegetation classification and mapping. The national Gap Analysis program is mapping actual vegetation to the formation level based

on the UNESCO classification system (Jennings 1993), and to Series within these formations based on dominant or co-dominant over-story species.

For this study we identified vegetation types by one to three over-story species, each contributing greater than 20% of relative canopy cover. The 20% cover criterion, which we selected to be consistent with the California Vegetation Type Mapping (VTM) survey (Wieslander 1946; see Colwell 1988, for overview), is lower than typically applied to define canopy dominance. For example, the CALVEG classification defines dominant as >50% (Parker and Matayas 1981). Payson et al. (1980) define Series based on a single dominant over-story species or genus. The ongoing California Native Plant Society Community Inventory is identifying Series primarily based on a single, overstory dominant, although a few series are based on two co-dominant species, and others are defined by environment (e.g., Alpine Series) (Sawyer 1993). For our purposes and at our 1:100,000 mapping scale, we found that use of single canopy dominants to type vegetation produced an unacceptable simplification of vegetation composition and pattern. For example, much of the chaparral vegetation in the Southwest Region would be mapped as Chamise or Scrub oak chaparral, masking systematic, regional variation in community composition. By using the 20% cover threshold, we retained information on one to three, and rarely four, canopy species that are dominant or co-dominant over several-to-many hectares. This area is much larger than plot sizes used in traditional vegetation studies. To avoid confusing these vegetation types with Series or Associations as defined by other systems, we refer to these combinations as *Species Assemblages*. In the field, species in an assemblage may be uniformly mixed or in a fine mosaic of patches, depending on the scale at which the pattern is observed. This means that in practice, species assemblages in our database can be a series recognized by existing classification systems, a combination of two or three recognized series, or previously unrecognized species combinations.

A map of actual vegetation was produced using summer 1990 Landsat Thematic Mapper (TM) satellite imagery, 1990 high altitude color infrared photography (1:58,000 scale), VTM maps based on field surveys conducted between 1928 and 1940, and miscellaneous recent vegetation maps and ground surveys. Details of the mapping process are provided in Davis (1991), and are only summarized here.

We did not have the resources to map individual stands of homogeneous vegetation. Instead, we have attempted to delimit "landscapes," which we defined as areas of one to many square kilometers in extent with uniform climate, physiography, substrate and disturbance regime, and covered by a single species assemblage or by a

mosaic of a few species assemblages associated with different sites (e.g., riparian zones, mesic slopes, xeric slopes). Landscape boundaries were mapped subjectively by photointerpretation of patterns in the satellite imagery. Final delineation of a landscape unit was an iterative process based on evidence from the satellite imagery, 1990 air photos, existing vegetation maps and field reconnaissance. The map was produced using a minimum mapping unit of 100 ha (1 km²), and the region was mapped into 2014 landscape units, or polygons.

TM imagery was resampled to the Albers equal-area projection with 100 meter resolution (i.e., 1 hectare pixels), and a false color composite of red, near-infrared and mid-infrared reflectance images was displayed on a video monitor. Obvious landscape boundaries were digitally drafted over the imagery based on image tone and texture. Ancillary information, especially air photos and VTM maps, was used to capture additional compositional changes in vegetation that were not visually obvious in the TM imagery. VTM maps were used to position landscape boundaries on vegetation gradients where no obvious break was visible on either the satellite imagery or in air photos. Two hundred and thirty polygons (excluding urban and agricultural areas) were checked in the field, primarily by roadside reconnaissance.

Using these various sources, a large amount of information was collected for each landscape unit (Table 1). Based on our concept of landscape, we recorded a primary species assemblage, which was the most widespread vegetation type or land use/land cover type in the polygon, a secondary type, and the fraction of the landscape covered by each type. We also recorded the most widespread wetland assemblage, which was usually riparian vegetation. Each species assemblage was defined by up to three dominant species. We also recorded the occurrence of minor overstory species of special conservation concern (e.g., *Juglans californica*, *Quercus engelmannii*, *Cupressus forbesii*).

Species data were derived from field survey, air photos or from the VTM maps. VTM information was used for areas where air photos provided no evidence of recent disturbance, based on the assumption that canopy dominants observed by VTM field crews have not changed over the past 50–60 years. We realize this is a tenuous assumption. We found during our field surveys that the assumption is usually valid for forest and hard chaparral types. Although the relative dominance of species may have changed over the interval, species that were mapped as co-dominants by VTM crews in the 1930's are still canopy dominants across the same landscape. The composition of soft chaparral and grassland types is not as stable over the same interval, and we made special efforts to view these types in the field or to find more current maps. Our

TABLE 1. DATA COMPILED FOR EACH VEGETATION MAP UNIT AND USED TO DERIVE MAPS OF SPECIES' DISTRIBUTIONS, NDDB PLANT COMMUNITIES, AND GAP ANALYSIS SPECIES ASSEMBLAGES.

Polygon ID, number
Primary vegetation
Dominant species 1
Codominant species 2
Codominant species 3
Canopy closure (4 classes)
Fraction of polygon occupied by primary type (10% intervals)
Secondary vegetation
Dominant species 1
Codominant species 2
Codominant species 3
Canopy closure
Fraction of polygon occupied by type
Presence/absence of 9 wetland habitat types (CA WHR types)
Primary wetland vegetation
Dominant species
Codominant species 1
Codominant species 2
Presence of canopy species of special status (narrow endemics, RTE species)
Evidence of disturbance (5 categories)
Source map(s) used in interpretation
Air photo ID number
Field visit
Analyst

landscape units are many square kilometers in extent, and canopy composition can vary greatly from site to site within a landscape. Thus the species assemblages that we have mapped record those species that most frequently dominate most sites in that landscape.

We have tried to account for fire dynamics by recording recent burns and by retaining information on the pre-burn dominants (e.g., an area of recently burned chamise chaparral that is presently dominated by herbs would be recorded as sparse chamise canopy co-dominated by annual herbs).

Rather than a multi-colored vegetation map, the information we have developed is better treated as a vegetation database linked to a set of areas. One can retrieve distribution data on individual species, unique combinations of species, or vegetation types defined by physiognomy and/or composition (Stoms et al. 1992). Although the database approach provides a more flexible framework for representing vegetational variation than the traditional vegetation map, it does not eliminate the need for classification in order to simplify and communicate results. We recorded 1013 unique species (or species/landuse) combinations in 2100 polygons. Many unusual species combinations occurred at the margins of the region in transitional

environments. Here we summarize distribution data for individual dominant species and based on plant communities as defined in the California NDDB (Holland 1986), which we derived from the database by an equivalence table assigning each species combination to a unique NDDB community. The criteria for class assignment in the NDDB classification system are qualitative and often not explicitly based on dominant overstory species. Where ambiguities existed, we assigned species combinations to more general types. For example, Holland (1986) identified four Sage Scrub community types (Venturan, Diegan, Diablan and Riversidian) that we necessarily aggregated into a single type.

Map accuracy assessment. Map accuracy can be assessed in many different ways, most commonly by comparing the map to ground observations for a set of sample "points" (Congalton 1991). This approach is not practical for small scale maps such as ours because of the sampling effort required to determine the actual map class at a point on the ground when the minimum mapping unit is 1 km². The size and limited accessibility of some parts of the study area also pose considerable financial and logistical challenges. For these reasons, we have not conducted a formal assessment of the accuracy of the vegetation database. Instead, we have attempted to provide a qualitative measure of map accuracy through roadside reconnaissance and by comparing our map with recent detailed vegetation maps that have been prepared for parts of the region. As noted above, 230 polygons were checked in the field. Less than 5% of the polygons that were visited needed replacement of the Primary or Secondary Series. Roughly one-half of the polygons required minor adjustments, such as a reversal of Primary and Secondary Series, or addition or deletion of a canopy co-dominant.

We compared our vegetation data to large scale vegetation maps that had been extensively field checked and were not used in preparing the Gap Analysis map. For instance, we compared our Coastal Sage Scrub Series to a map prepared with a 1 ha MMU by Regional Environmental Consultants (RECON) for coastal San Diego County (Stine et al. in press). RECON mapped 1625 stands of coastal sage scrub, compared to 105 landscapes containing coastal sage scrub in the Gap Analysis map. Ninety-nine % of coastal scrub in patches larger than 100 ha was represented in both maps. One thousand three hundred, eighty-three RECON polygons fell outside landscapes that we had mapped as containing Coastal Sage Scrub. However, nearly all of these RECON polygons were small fragments of coastal sage scrub in urban or agricultural landscapes, and 75% were smaller than 10 ha, thus falling well below the grain size of our analysis.

We have also compared our map to very detailed vegetation maps (MMU <0.25 ha) prepared for southwestern San Diego County as

part of the Multi-Species Conservation Planning (MSCP) program (Ogden Environmental and Energy Services 1993). A comparison of 138 random points on the two maps shows 87% agreement (i.e., either Primary or Secondary designation of the Gap map is in accord with the MSCP designation) and only 5% are larger polygons (i.e., > 10 ha) that disagree.

In summary, the vegetation database has inaccuracies but is generally in high agreement with other, recent vegetation maps. However, it is a highly generalized abstraction of vegetation pattern that can serve only for broad regional assessments and inventories. The database is being distributed in both digital and analogue form to local botanists and we fully anticipate that the map will undergo periodic revision based on feedback from local experts. Those revisions should not significantly affect the general results reported here.

Land management. All lands are managed by humans, and these management activities can be of primary importance in determining the status and trends in species and communities. Unfortunately, ecologically meaningful information on management activities is difficult, if not impossible, to obtain for many areas of the state. In the absence of better information, we have used land ownership and administrative designation as surrogates for management. For the purposes of Gap Analysis, we distinguish three levels of management (modified from Scott et al. 1993):

Level 1 management: An area with biodiversity conservation as a defined management objective, that is essentially maintained in its natural state and within which natural disturbance events are either allowed to proceed without interference or are mimicked through management (comparable to the California Heritage Division's Protected and Semi-Protected designations). Examples include national parks, TNC reserves, federal wilderness areas, U.S. Forest Service Research Natural Areas, and BLM Areas of Critical Environmental Concern.

Level 2 management: Most non-designated public lands, including National Forests, military lands, county parks, and so on. Legal mandates prevent permanent conversion to anthropogenic habitat types (with some exceptions, such as tree plantations) and confer protection to populations of federally listed and/or candidate species. Habitats are potentially subject to competing consumptive uses. Sites generally have a manager or managing agency capable of protecting elements of biodiversity. (Heritage Division designation, Unprotected.)

Level 3 management: Other private lands without existing easement or irrevocable management agreement that maintains native

species and natural communities, and which are managed primarily or exclusively for intensive human activity. The Heritage Division does not define this category.

In collaboration with the California Department of Fish and Game Natural Heritage Division, we developed a map of land ownership at a scale commensurate with the objectives of Gap Analysis (200 ha minimum mapping unit for most areas, 80 ha for coastal and wetland reserves) (Beardsley and Stoms 1993). The base map is land ownership as portrayed in 1:100,000 Bureau of Land Management Surface Management Status maps. A statewide, digital coverage was provided to us by the Teale Data Center. We updated this coverage to reflect recent changes in land ownership, and then added administrative boundaries of managed areas such as wilderness areas and research natural areas. To determine these boundaries, we consulted National Forest maps and USGS topographic maps, and contacted many agencies, conservation organizations, and land trusts. Information tabulated for each mapped ownership/management unit includes managing agency, management level with respect to biodiversity conservation, a managed area code assigned by the Heritage Division, the source of the digital boundary lines, and the date of establishment.

Identifying species and communities at risk. The premise of Gap Analysis is that biological resources at risk can be identified by their ownership/management profile as generated by GIS overlay of 1:100,000 scale maps. To test this premise, we compared the ownership profiles of plant communities that are considered at risk by the Natural Heritage Division of the state Department of Fish and Game. Using a look-up table to classify our map units into NDDB community types, we derived 64 mapped communities (out of 89 recognized in the region), 61 of which occupied more than 2 square kilometers in our representation. The proportion of each community's distribution in Level 1 management versus private land is shown in Figure 2. The mapped distribution of threatened upland types is significantly different than the types in general. All show less than 10% of the distribution in Level 1 Management, and 5/6 show at least two-thirds of their current extent on private lands. Six threatened wetland types are less distinctive, as would be expected given the scale of the vegetation map. Nevertheless, threatened wetland communities also show the same general pattern of being predominantly on private lands and with little representation in existing Level 1 managed areas.

These results reinforce the caveat stated above that Gap Analysis data are not appropriate for assessing highly localized community types and widespread types that typically occur in small patches, such as many wetland types. However, Figure 2 supports our premise

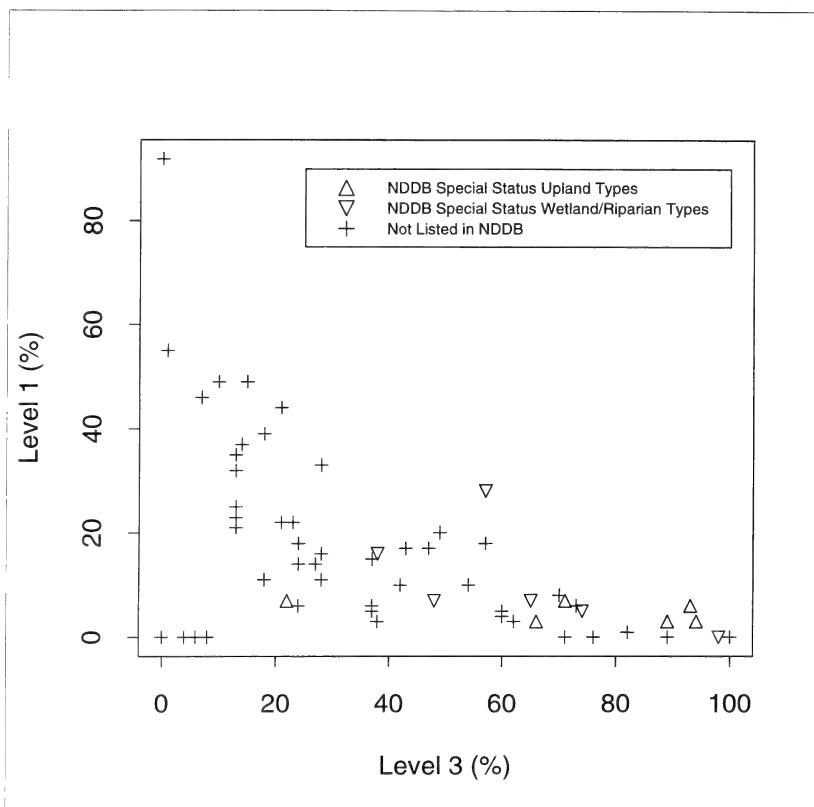


FIG. 2. Plot of the proportion of 64 Natural Communities, as defined by Holland (1986), in Level 1 (managed primarily for biodiversity) versus Level 3 (unrestricted private lands). Diamonds identify those communities that are considered by the Heritage Division of California Department of Fish and Games to be threatened or of special concern.

that the Gap Analysis approach can be used to identify more widespread upland plant communities at risk. Guided by these results, we adopted the following criteria for identifying communities at risk:

1. Less than 10% of the mapped distribution is in Level 1 areas, and the species or community type is endemic to the region, and the mapped distribution covers more than 100 km²,

or

2. over 70% of the mapped distribution is in Level 3 areas.

RESULTS

Land ownership and management. Fifty-four Level 1 managed areas were identified that meet the minimum mapping unit size in

TABLE 2. AREA BY MANAGEMENT LEVEL IN THE SOUTHWESTERN CALIFORNIA REGION. (Source: California Gap Analysis Database.) Also tabulated are the area and management status of areas mapped as Significant Natural Areas (SNA's) by the Inter-agency Natural Areas Coordinating Committee (data courtesy of the State of California Natural Heritage Division, Department of Fish and Game). Discrepancy in Total from the sum of Level 1 through 3 is due to small managed areas whose area is below the minimum mapping unit (MMU) of 200 ha.

Level	All land area (in ha)	Percent of total land area	SNA's area (in ha)	Percent of total SNA area
Level 1	330,655	9.8%	57,008	12.1%
Level 2	1,030,531	30.5%	125,682	26.7%
Level 3	2,021,197	59.7%	287,212	61.1%
Total	3,383,160	100%	470,407	100%

the Southwestern California region. A large fraction of Level 1 land is National Forest Wilderness Areas, with 226,185 hectares in 14 areas. State Parks, including Reserves and Wilderness Areas, are the second largest category of Level 1 areas, totaling 56,204 hectares. In summary, Level 1 areas total 324,773 ha or 9.6% of the region. 30% of the region is other public lands managed at Level 2, while the remaining 60% is Level 3 (Table 2). Roughly 47% of Level 3 lands support natural vegetation cover, while the remainder were mapped as urban, residential or agricultural.

From the "date of establishment" attribute in the database, we were able to compile a picture of the increase in Level 1 managed areas over time. Roughly one-quarter of the current Level 1 managed area was established prior to 1960. The wilderness system was expanded during the 1960's, again in 1984, and most recently in 1992 with the designation of several large wilderness areas in Los Padres National Forest.

Management status differs systematically among elevation zones. Elevations below 1500 m (89% of the region), where most urban and agricultural development are located, are predominantly private land, whereas elevations between 1500 m and 2500 m (10% of the region) are primarily public lands, mainly in Level 2 management. The majority of land above 2500 meters is in level 1 management, and in fact more than 90 percent of the highest elevation zone is in Level 1 management (predominantly National Forest wilderness areas). However, lands above 2500 meters account for slightly less than 1% of the total region.

Distribution and management status of dominant species and communities.

- 1) Herbaceous vegetation—We were unable to distinguish herbaceous plant species and community types beyond very general

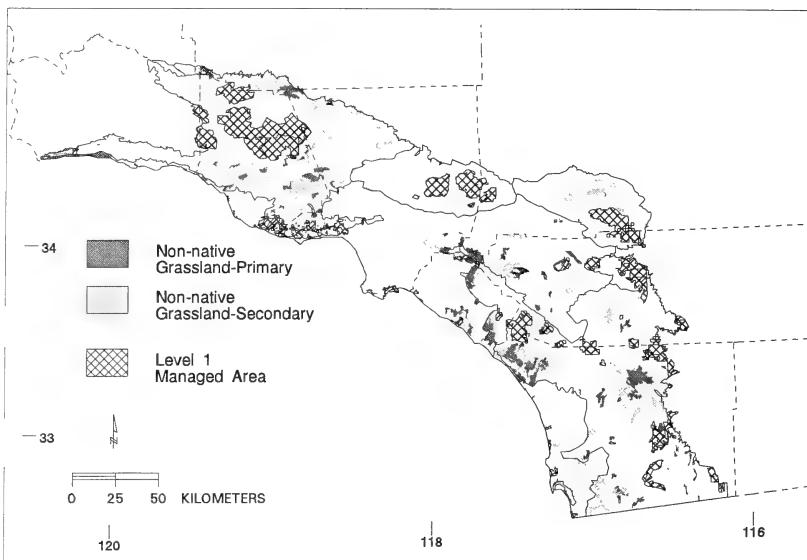


FIG. 3. Distribution of landscapes where Non-native Grassland (#42200) is the primary (dark shading) or secondary (light shading) upland vegetation type. Also shown are county boundaries (broken lines), geographic subregions (solid lines) and Level 1 managed areas (hatched pattern).

classes. For example, we classified practically all grasslands as "Non-native" despite the fact that many of these areas contain sizeable populations of native grasses and forbs. Thus our estimate of the extent of the Valley Needlegrass community is undoubtedly too low (Appendix B). Keeley (1990) provides a much more detailed assessment of the distribution and conservation status of native grasslands. However, we would call attention to the fact that nearly three-fourths of non-native grassland in the region is privately held, and only 6% is in Level 1 areas (Fig. 3). Although dominated by exotic species, these grasslands can be rich in native plant species and are habitat to many animal species. Recent efforts to preserve grassland habitats for the Stephens' kangaroo rat (*Dipodomys stephensi*) in the Riverside Basin attest the ecological significance of this community type. However, annual grasslands in other parts of the region are generally not considered a conservation priority. Our data suggest that from a regional perspective non-native grasslands appear to be at risk.

2) Sagebrush steppe species and vegetation types—Plant communities dominated by *Artemisia tridentata*, *Chrysothamnus nauseosus* or *C. parryi* occur along northern and northeastern margins of the region, and are concentrated in the upper Cuyama Valley,

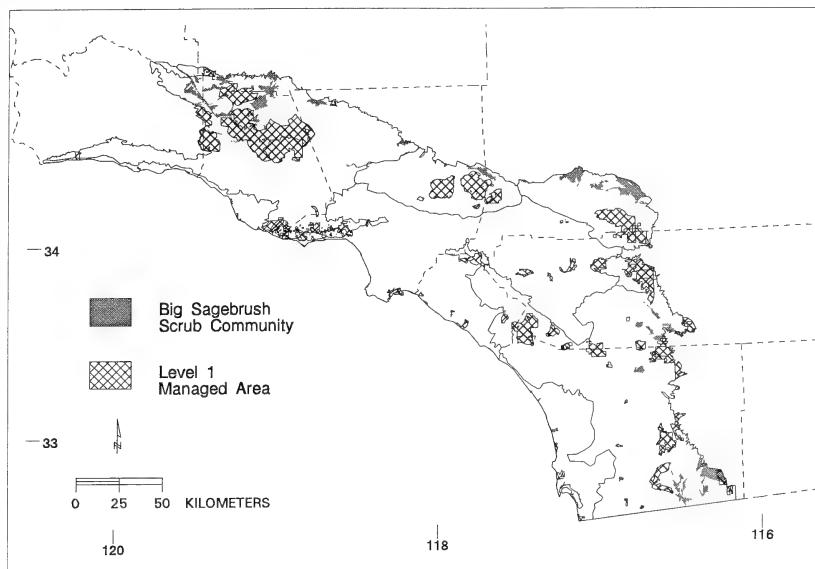


FIG. 4. Distribution of landscapes where the Big Sagebrush Scrub Community Type (#35210) is the primary or secondary upland vegetation type. Also shown are county boundaries (broken lines), geographic subregions (solid lines) and Level 1 managed areas (hatched pattern).

Lockwood Valley, eastern San Bernardino Mountains, locally in the Anza Valley, and in the extreme southeastern corner of the region (Fig. 4). Roughly 60% of the area occupied by sagebrush steppe is multiple-use public land, and less than 5% occurs in Level 1 managed areas. It appears that nearly all sagebrush steppe in the region is subject to grazing. Some areas are already the focus of conservation efforts aimed at protecting threatened and endangered species. For example, the Pebble Plains, in the northeastern San Bernardino Mountains, are habitat to candidate endangered species such as *Castilleja cinerea* and *Astragalus leucolobus*. Based on current land ownership and managed patterns, sagebrush steppe in this region appears to be at high risk and deserving of more conservation research and management.

3) Soft chaparral—All soft chaparral species and communities occur predominantly on private lands. Soft chaparral in California is largely confined to this region, although variations with different species composition extend north along the coast to beyond the San Francisco Bay. Once very common and widespread, particularly in the south coast subregion, the type has been fragmented and its extent reduced severely by development of coastal habitats (O'Leary 1990). Much conservation effort is focused on areas in Orange, Riv-

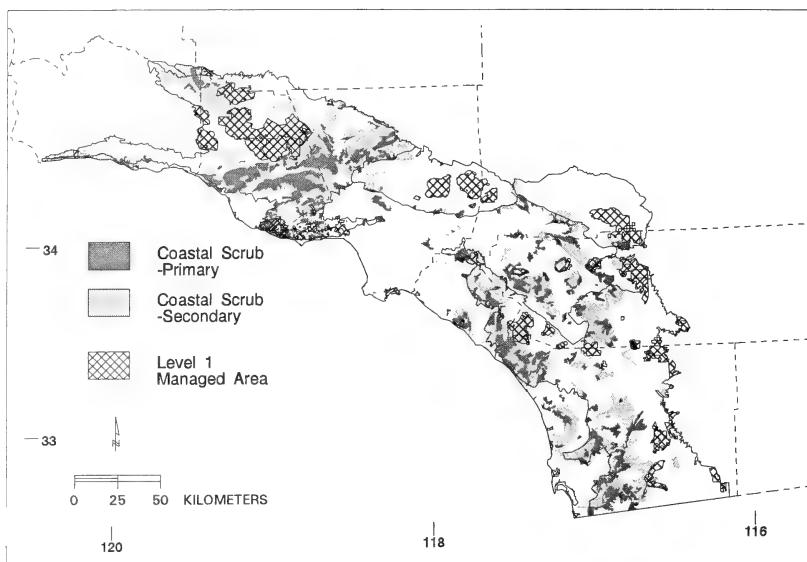


FIG. 5. Distribution of landscape where the Coastal Scrub Community Type (#32000) is the primary (dark shading) or secondary (light shading) upland vegetation type. Also shown are county boundaries (broken lines), geographic subregions (solid lines) and Level 1 managed areas (hatched pattern).

erside, and San Diego counties that are habitat for the threatened California gnatcatcher (*Polioptila californica*) (Brussard and Murphy 1992). Our analysis highlights the need to consider more northerly elements as well. For example, practically all landscapes dominated by *Salvia leucophylla* are in the western Transverse ranges, north of the current range of the gnatcatcher (Appendix A). Nearly all (87.3%) of the mapped distribution of this species is privately owned.

The CNDDB coastal scrub community is widespread (3908 km²), but 71% is on Level 3 lands and only 7% is on Level 1 lands (Fig. 5 and Appendix B). We mapped 23 major coastal scrub species assemblages (not shown) over about 10% of the region, perhaps less than 15% of their historical coverage (Westman 1981). Soft chaparral dominated by *Artemisia californica* appears most at risk. Other coastal scrub types do not have much higher percent in protected status; the highest percentage in Level 1 (excluding *Yucca whipplei*, which has a very small coverage) is 7.1% for *Salvia apiana*.

4) Chaparral—Chaparral is the dominant and characteristic vegetation of this region. Seventeen natural community types and 64 species assemblages were identified covering over 12,057 km², about 36% of the current land cover of the region (including urban and agricultural lands). *Adenostoma fasciculatum* is the most widespread

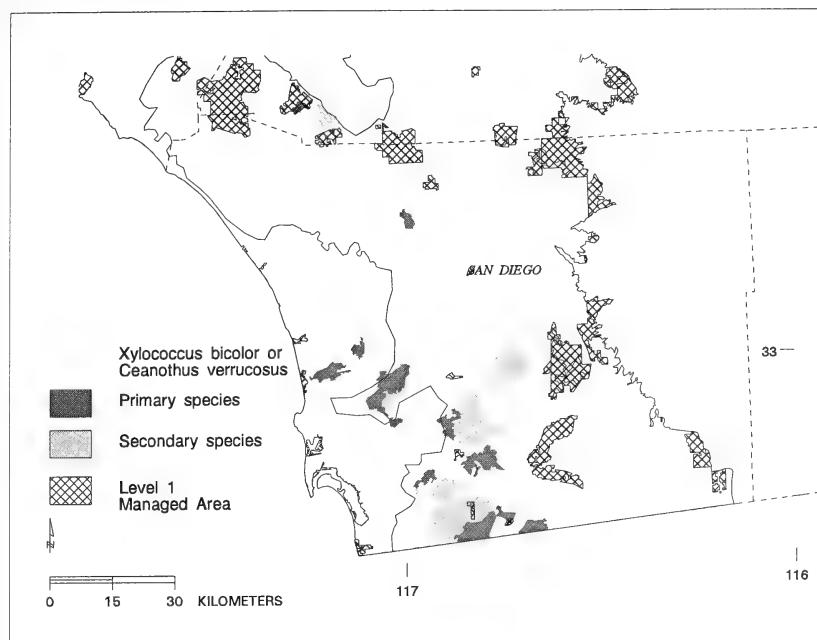


FIG. 6. Distribution of landscapes where either *Xylococcus bicolor* or *Ceanothus verrucosus* is the primary (dark shading) or secondary (light shading) upland vegetation type. Also shown are county boundaries (broken lines), geographic subregions (solid lines) and Level 1 managed areas (hatched pattern).

chaparral species in the region, occurring as a dominant or co-dominant on almost 8000 km². It is associated with a number of different species, the most frequent being *Ceanothus crassifolius*, *C. greggii*, *Adenostoma sparsifolium*, and *Arctostaphylos glandulosa*. Many of these assemblages show little overlap and are associated with specific subregions. For example, *A. fasciculatum/C. crassifolius* dominates mid-elevations of the San Bernardino, San Gabriel, and Santa Ana mountains. *Adenostoma fasciculatum/C. greggii* var. *perplexans* is widespread in the Peninsular Ranges, and *A. fasciculatum/A. sparsifolium* occurs extensively along the western slopes of the Santa Rosa Mountains and more locally in the Santa Monica Mountains.

The large majority of the chaparral species and communities appear to be either widespread and/or well represented (i.e., over 10%) in the Level 1 areas. Some taxa are also relatively uncommon and underprotected in this region (e.g., *Fraxinus dipetala* and *Ceanothus sordidus* = *C. oliganthus* var. *sordidus*). Several assemblages are both uncommon and underprotected, notably those containing *Xylococcus bicolor* and *Ceanothus verrucosus*, which occur at the southern end of the region (Fig. 6). The percent in Level 1 management

for *X. bicolor* and *C. verrucosus* are 3.4% of 219 km² and <0.01% of 16 km², respectively.

We mapped 17 CNDB chaparral types out of 22 known to occur in this region. Of the 5 remaining community types, Tobacco brush and Bush chinquipin chaparral are localized at higher elevations in this region. Poison oak chaparral is currently not well defined, although it is probably a more distinct entity north of this region. Southern maritime chaparral and Alluvial fan chaparral are restricted to this region. We were unable to map Southern maritime chaparral from our data using the description by Holland (1986), and the latter is too localized to be represented at our map scale.

5) Hardwood forest/woodland—There are five major hardwood woodland types characteristic of this region. *Quercus agrifolia* is distributed throughout the region and in association with a number of other co-dominant species. Most series types and the overall distribution of this species are poorly represented in protected areas, and conversion to urban land use appears to be one of the major causes of decline in these types (e.g., Scheidlinger and Zedler 1980). *Quercus engelmannii* is endemic to this region and is also significantly under-represented in Level 1 areas (Fig. 7). Recently Scott (1991) analyzed the geographic distribution of this species based on 1:24,000 maps that he prepared from air photos. He estimated that *Q. engelmannii* occurs over 31,500 ha, compared to our estimate of 23,600 ha. The discrepancy appears mainly due to the differences in map scale rather than classification, given that his mapped stands fall almost entirely within our mapped landscapes. Scott called attention to the poor representation of the species in existing reserves, a pattern that we also observed (<3.5% in Level 1 areas), despite the recent establishment of significant new reserves such as The Nature Conservancy's Santa Rosa Plateau Reserve.

The various riparian woodland types are usually found in patches too small to be detected with the techniques employed by the Gap project. Nevertheless these types appear to be poorly represented (0.2 to 7.2%) in Level 1 areas. *Quercus chrysolepis*, and to a lesser extent *Quercus kelloggii*, are widely distributed in the region and throughout California, and generally well represented in Level 1 protected areas.

More localized woodland species include *Quercus lobata*, *Quercus douglasii*, *Quercus wislizenii*, *Arbutus menziesii*, and *Juglans californica*. While most of these species are more widely distributed in other regions of California, the southern California black walnut (var. *californica*) is almost entirely restricted to this region. The current distribution of this species is highly fragmented and almost entirely (89.3%) on private land, with remnant populations in the Santa Clara River drainage, Simi Hills, Santa Susana Mountains, Santa Monica Mountains, San Jose Hills, Puente Hills, and Chino

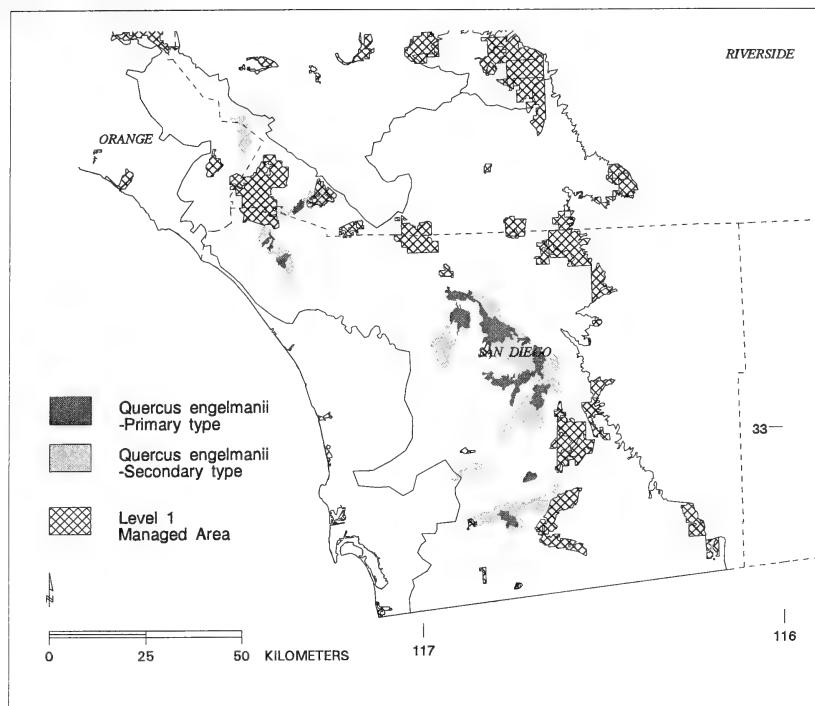


FIG. 7. Distribution of landscapes where *Quercus engelmannii* occurs as a canopy dominant or co-dominant in the primary (dark shading) or secondary (light shading) upland vegetation type (usually Open or Dense Engelmann oak woodland or Coast live oak woodland). Also shown are county boundaries (broken lines), geographic subregions (solid lines) and Level 1 managed areas (hatched pattern).

Hills. Quinn (1990) provides a detailed analysis of the distribution, ecology and conservation status of this type, and emphasizes the need for immediate conservation action in the face of imminent urbanization of many remaining habitats.

6) Conifer forest/woodland—*Pseudostuga macrocarpa* and, to a lesser extent, *Pinus coulteri* are largely restricted to and characteristic of this region. They generally occur from 500 m to 1500 m, but *P. macrocarpa* is concentrated in canyons and steep north-facing slopes, whereas *P. coulteri* occupies a range of topographic sites. Thirty four percent of the mapped distribution of *P. macrocarpa* is in Level 1 areas (Appendix A), and 40.7% of the widespread species assemblage, Big cone spruce/canyon live oak, is in Level 1 areas. 22.2% of the mapped distribution of *P. coulteri* is on Level 1 lands. At slightly higher elevations, *Pinus ponderosa*, *P. lambertiana*, and *Calocedrus decurrens* are well represented in Level 1 areas (38.1%, 41.8%,

and 13.3%, respectively), with the vast majority of the remaining distribution on Level 2 lands. Highest elevations are dominated by *Abies concolor*, *Pinus jeffreyi*, *Pinus contorta* var. *murrayana*, and *Pinus flexilis*. These vegetation types are among the best protected types in the region, with 22.2% to 91.1% of mapped distributions in Level 1 areas.

Pinus monophylla and *Juniperus californica* are prominent at the region boundaries adjoining the Desert and Central Valley regions. Both appear to be reasonably well represented in Level 1 areas at 14.2% and 15.6%, respectively (Appendix A). The Pinyon pine/California juniper assemblage is widespread in the upper Cuyama Valley and in other parts of the Transverse Ranges, and has 23.4% in Level 1 areas. Most other lands that include these two species are in Level 2 management.

Several other coniferous forest species are found only peripherally in this region. *Pinus attenuata*, *P. sabiniana*, and *J. occidentalis* are rare here and more widespread in adjoining regions. Two endemic conifers, *Cupressus forbesii*, and *C. arizonica* ssp. *arizonica* are restricted to very local sites and difficult to detect using our method. Both are worthy of conservation attention based on existing information (Oberbauer 1990).

Natural heritage division significant natural areas. Significant Natural Areas (SNA's) are a designation of the California Fish and Game's Land and Natural Areas Program (LNAP) for locations with concentrations of rare or endangered biota. A SNA must meet at least one of three criteria: extremely rare elements of biodiversity, ensembles of three or more elements, or best examples of elements (Hoshovsky 1988). Some SNA's are mapped as circles drawn around a point where a rare element occurs rather than as irregular polygons drawn along natural or ownership boundaries. The LNAP has produced a digital map of the 1992 version of the SNA inventory that was provided to the California Gap Analysis project. An overlay of the Gap Analysis Management layer with the SNA map indicates that the percentage of SNA's in each level closely matches that of the region as a whole (Table 2). This is indicative of the fact that biological reserves have historically been established without systematic attention to their biotic composition. The primary opportunities for protecting SNA's on public lands are the national forests (14% of the total area in SNA's) and military bases (7.5% of SNA lands).

DISCUSSION

Limitations of the methods. Gap Analysis provides a regional overview of the distribution and ownership profile of major terrestrial plant species and communities. The method is not suited to

the analysis of most wetland types, dune communities, or other communities that are restricted to very localized environments. The vegetation mapping technique is well suited to analysis of shrubs and trees, but provides little or no information on the distribution of herbaceous species.

Estimates of area made from maps are very sensitive to map scale and mapping methods. Our map is less sensitive because we have recorded proportions of types within polygons. Nevertheless, our estimates of the extent of species and types are only useful for comparing among types on our map, and are not the same as areas calculated from maps prepared at another scale. Similarly, our maps of vegetation and land ownership were prepared commensurately for direct overlay and comparison, but ownership profiles of vegetation types would be somewhat different if either map was prepared using a different minimum mapping unit.

Land ownership/management profiles provide a crude measure of risk of development or resource over-exploitation. Species and communities can also be at risk due to climatic change, introduced competitors and pathogens, and many other ecological factors. For instance, subalpine forests may be extremely well protected in the region but at high risk due to global warming. Furthermore, there is wide variation in land management practices within each of the three categories. Some private lands are well managed for the maintenance of plant diversity, but some reserves may be managed in a way that threatens the persistence of selected species. Private land management also depends heavily on zoning status, and county zoning data are required to conduct a fuller analysis of present and possible future management of private lands. We are presently collaborating with the Southern California Association of Governments to conduct such an analysis. Similarly, land management on public lands ultimately should be analyzed within individual administrative units (e.g., individual national forests), and we are distributing our data to federal and state agencies to support these more detailed analyses.

The static nature of the Gap Analysis data also limits their utility in conservation risk assessment. Our database provides a snapshot of a region in which land cover and land ownership are both very dynamic and where trend data would be especially useful. VTM survey data collected a half century ago provide some opportunity for such trend analyses, and we intend to pursue such comparisons, which must remain qualitative given the nature of VTM and Gap Analysis data. For example, Figure 8 shows such a comparison for *Artemesia californica* in the southeastern portion of the region. The species is greatly reduced from the distribution mapped in the 1930's, especially in the San Diego metropolitan area, the area from Lake Elsinore to Temecula, and the Riverside Basin.

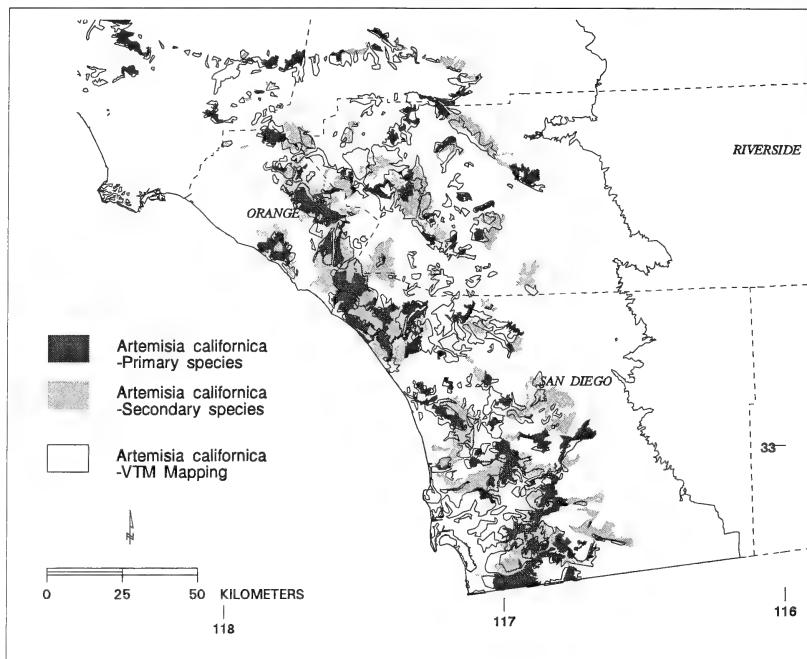


FIG. 8. Generalized distribution of *Artemesia californica* as mapped by VTM field crews between 1928 and 1940 (solid lines) compared to 1990 distribution as represented in the Gap Analysis database. Areas where the species occurred as a canopy co-dominant in the primary vegetation type (dark shading) and the secondary type (light shading) are shown. The digital VTM map was produced and described by Westman (1991).

Priority communities and species. Tables 3 and 4 list species and plant communities that we consider to be at risk based on the criteria defined above. Communities restricted largely to the lower elevations, such as non-native grasslands and the coastal sage scrub types, are clearly at considerable risk. Roughly 88% of areas below 500 m are in Level 3 management (i.e., privately owned). A majority of the lands at these elevations have already been converted to agricultural or urban uses and most of the remaining lands are threatened with future urbanization.

All extensive riparian communities, particularly those confined largely to low elevations such as mule fat scrub and southern arroyo willow, are already well known to be at risk (Bowler 1990), as are coastal wetlands (Ferren 1990). Conservation initiatives are already underway for most of these communities. Especially alarming is the condition of the California black walnut woodlands. The southern variety of this species is endemic to this region and its current dis-

TABLE 3. NATURAL COMMUNITIES IDENTIFIED AT RISK USING GAP ANALYSIS CRITERIA. Community codes are from NDDB. Communities are ordered from highest to lowest relative extent on private lands. Asterisks indicate community types whose mapped distribution totals less than 50 km². Other communities identified by the Natural Heritage Division as threatened or endangered but not detected by the Gap Analysis method are listed separately.

Code	Natural community name
71130	Valley Oak Woodland*
42110	Valley Needlegrass Grassland*
71210	California Walnut Woodland
37G00	Coastal Sage-Chaparral Scrub
71410	Digger Pine-Oak Woodland*
42200	Non-Native Grassland
32000	Coastal Sage Scrub
71160	Coast Live Oak Woodland
81310	Coast Live Oak Forest
71182	Engelmann Oak Woodland
37120	Southern Mixed Chaparral
37300	Redshanks Chaparral
35210	Big Sagebrush Scrub
37B00	Upper Sonoran Manzanita Chaparral
83330	Southern Interior Cypress Forest*
72210	Mojavean Pinon Woodland*
72110	Northern Juniper Woodland
Other threatened or endangered plant communities	
21330	Southern Dune Scrub
32400	Maritime Succulent Scrub
32720	Riversidian Alluvial Fan Sage Scrub
37C30	Southern Maritime Chaparral
42300	Wildflower Field
44310	Southern Interior Basalt Flow Vernal Pool
44321	San Diego Mesa Hardpan Vernal Pool
44322	San Diego Mesa Claypan Vernal Pool
47000	Pebble Plains
52120	Southern Coastal Salt Marsh
52200	Coastal Brackish Marsh
52410	Coastal and Valley Freshwater Marsh
61330	Southern Cottonwood-Willow Riparian Forest
	Canyon Live Oak Ravine Forest
62100	Sycamore Alluvial Woodland
62400	Southern Sycamore-Alder Riparian Woodland
63320	Southern Willow Scrub
63300	Southern Riparian Scrub
81820	Mainland Cherry Forest
83140	Torrey Pine Forest

tribution is highly fragmented and reduced compared with its original distribution.

Sagebrush steppe shrublands, although widespread elsewhere in California and other western states, appear vulnerable in this region. A significant proportion of the sagebrush steppe habitat is on Level

TABLE 4. DOMINANT PLANT SPECIES CONSIDERED AT RISK BASED ON GAP ANALYSIS CRITERIA. Species are grouped by community type with which they are most associated. * Fairly rare in this region but widespread in California, possibly rare associations in this region. ** Widespread taxon in California, but possibly rare ecotypes in this region. *** Rare local endemic, difficult to map at this level of resolution. **** Some associations are significantly underrepresented on Level 1 lands.

Coastal Sage Scrub	Hardwood Forest/Woodland
<i>Eriogonum fasciculatum</i>	<i>Quercus agrifolia</i> *
<i>Salvia apiana</i>	<i>Quercus engelmannii</i>
<i>Salvia leucophylla</i>	<i>Quercus kelloggii</i> *
<i>Salvia mellifera</i>	<i>Quercus lobata</i> *
<i>Malosma laurina</i>	<i>Juglans californica</i>
<i>Artemesia californica</i>	All riparian woodlands
<i>Encelia californica</i>	
Sagebrush Steppe Scrub	Conifer Forest/Woodland
<i>Encelia farinosa</i> *	<i>Cupressus forbesii</i>
<i>Chrysothamnus nauseosus</i> *	<i>Juniperus occidentalis</i> *
<i>Artemesia tridentata</i> *	<i>Juniperus californica</i>
<i>Pinus sabiniana</i> *	
Chaparral Shrubs	
<i>Arctostaphylos glandulosa</i> **	
<i>Xylococcus bicolor</i>	
<i>Prunus illicifolia</i> *	
<i>Ceanothus oliganthus</i> var. <i>sorediatus</i> *	
<i>Ceanothus tomentosus</i>	
<i>Ceanothus verrucosus</i> ***	
<i>Adenostoma sparsifolium</i> ****	

2 lands, and conservation concern for these communities can probably be adequately addressed by the public land managing agencies. Species and communities at higher elevations, especially montane chaparral and coniferous forest types, are generally well represented in Level 1 protected areas.

With the exception of canyon live oak and perhaps interior live oak, all other oak woodlands appear to be at risk now or over the next one or two decades. In contrast, most of the chaparral communities appear to be reasonably secure. They are generally found on steeper slopes, largely on public lands, and with at least 10% and often >20% in Level 1 status. However there are a wide variety of chaparral types in this region, and we should not take the conservation of all for granted. A number of chaparral species/communities are endemic or largely restricted to this region and there may be components of chaparral that may be at some risk.

Priority areas for conservation planning. Many different criteria have been used to prioritize areas for more detailed conservation planning and action, for example:

1. concentration of threatened and endangered taxa

2. concentration of threatened and endangered communities
3. concentration of narrowly endemic species
4. high taxonomic richness
5. high ecological diversity
6. extensive and/or well connected natural areas containing one or more taxa and/or communities of concern
7. areas that are environmentally or biotically distinctive or unique

Experience shows that the geographic distribution of priority areas can vary significantly depending on the criteria, the spatial scale of the analysis (e.g., Stoms 1992), and the taxonomic group(s) under consideration (e.g., Prendergast et al. 1993). Our Gap Analysis has identified relatively widespread upland plant species and communities that appear to be at risk as a function of land ownership and management status (criterion 6, above). We have not focused on locally endemic taxa nor on species already recognized as threatened or endangered. Figure 9 maps the density of threatened or endangered communities or plant taxa in 7.5 minute quadrangles, as represented in the California NDDB, as well as the percent of the quadrangle occupied by communities identified as at-risk by Gap Analysis. Patterns of the three criteria are quite distinctive, and only the Poway quad, which includes area between Poway and La Mesa in San Diego County, scores high on all three criteria. Western San Diego County, which has already undertaken an ambitious multi-species conservation planning effort, is striking for its concentration of threatened and endangered taxa and communities. The eastern edge of the region along the desert margin is distinctive for areas that contain concentrations of threatened taxa with low values for NDDB or Gap communities, while the northern region, notably the Santa Clara River Basin, contains many quads with large numbers of NDDB communities but low concentrations of NDDB plant taxa or Gap communities-at-risk.

From an ecosystem planning perspective, quads that contain high numbers of NDDB communities and where a large percentage is mapped by Gap Analysis as communities-at-risk seem likely candidates for new, extensive biodiversity management areas. These include the following quadrangles and areas:

- San Clemente, Canada Gobernadora and Oceanside quads (Santa Margarita River, Camp Pendleton)
- Beaumont quad (San Gorgonio Pass, foothills of San Bernardino and San Jacinto Mountains)
- Lake Mathews quad (Lake Mathews to Lake Elsinore)
- Piru, Simi, and Santa Susana quads (Santa Clara floodplain, Sespe and Piru Canyons, Oak Ridge to Santa Susana Mountains)
- Calabasas quad (Simi and Agoura Hills)

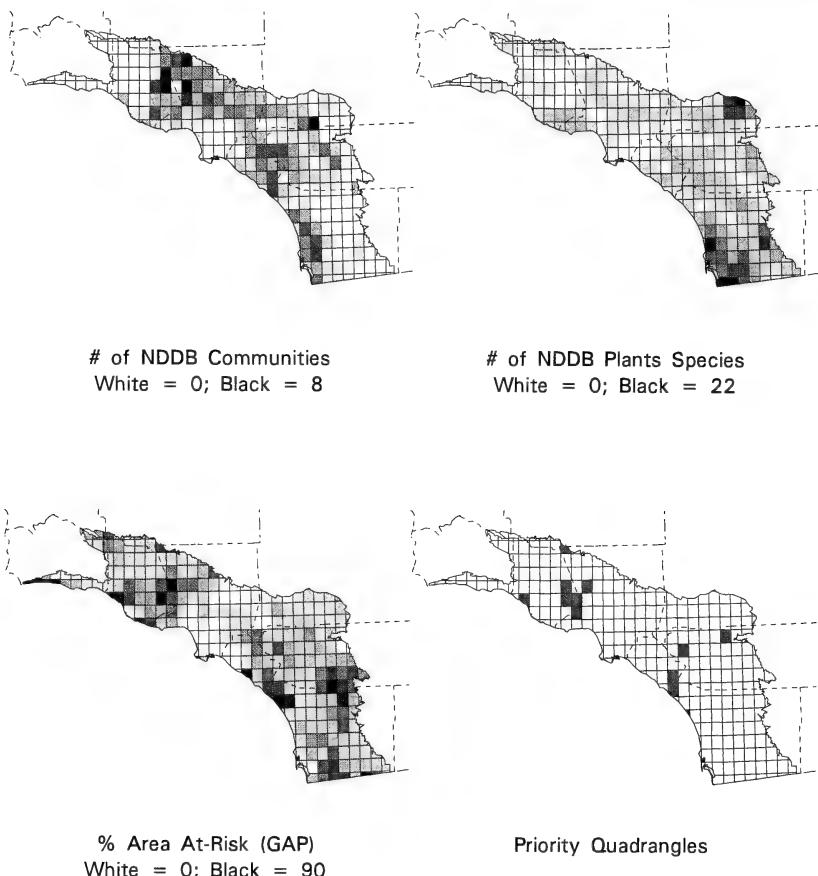


FIG. 9. Comparison of mapped patterns in three different conservation assessment criteria at the scale of 7.5 minute USGS quadrangle in the Southwestern California region. Criteria include 1) the number of plant communities at risk occurring in each quad, based on the California Natural Diversity Database (NDDB), 2) the number of threatened or endangered plant species occurring in each quad based on NDDB, 3) the percent of the quad occupied by plant communities deemed at risked as defined and mapped by Gap Analysis, and 4) quadrangles that rank highly in all three criteria for conservation activities.

- Ventura quad (lower Ventura River floodplain and surrounding slopes)
- Lebec quad (I5 corridor and slopes north of Castaic Lake to Grapevine (Tejon Pass))

The Nature Conservancy of California (TNC) recently conducted a conservation analysis of the Southwest region and identified priority areas based on the occurrence of 1) highly endangered species,

2) rare, threatened or declining communities, 3) large-landscape wildlife species, and 4) ensembles of three or more globally endangered species (California Nature Conservancy 1993). Using these criteria they identified 65 sites, 27 of which were considered critical for inclusion in a bioregional conservation strategy. Many of their sites fall within areas that are also of high priority based on the distribution of Gap communities-at-risk, especially in vicinity of Camp Pendleton, Otay Mesa in San Diego County, Lake Henshaw to Julian, and the western footslopes of the San Jacinto and Santa Rosa mountains. TNC sites that are also identified based on both NDDB community occurrence data and Gap Analysis data include the Santa Margarita River, San Mateo Creek, Miramar Mesa, Santa Clara floodplain near Fillmore, Sespe and Piru canyons, and Tejon Pass. The convergence of conservation priorities based on plant and animal species, threatened and endangered plant communities, and communities at risk, makes the case for immediate conservation action in these areas especially compelling.

ACKNOWLEDGMENTS

The California Gap Analysis project is being funded under contracts with the National Fish and Wildlife Foundation, Southern California Edison Company, the Idaho Cooperative Fish and Wildlife Research Unit, and the U.S. Forest Service Sierra Nevada Ecosystem Project. Their support is gratefully acknowledged. Special thanks to Whitney Tilt of the National Fish and Wildlife Foundation, Ken Hofmann and Dan Boatwright of the Hofmann Company, and John Palmer of Southern California Edison Company for their support and contract management. Research funds and computing equipment have also been provided by a generous grant from the IBM Corporation Environmental Research Program, under the direction of Dr. Joseph E. Sarsenski. The Southern California Association of Governments and the California Department of Fish and Game have also provided funding for the California Gap Analysis project. The Gap Analysis of the Southwestern region has benefited from collaboration and support from numerous public and private organizations, especially UCSB Map and Imagery Library, the Strategic Planning Program of the California Department of Forestry and Fire Protection, Teale Data Center, the Natural Heritage Division of the Department of Fish & Game (CDF&G), San Diego Association of Governments, Southern California Association of Governments, USDA Forest Service, Santa Monica Mountains National Recreation Area, Bureau of Land Management, California Nature Conservancy, UCSB Remote Sensing Research Unit, Metropolitan Water District, Recon Associates, Ogden Environmental and Energy Services, and Camp Pendleton Marine Base. Many individuals have also contributed to the project. Special thanks to J. Michael Scott, Blair Csuti, John Estes, Kent Smith, Barbara Allen-Diaz, Reg Barrett, Jim Quinn, Bob Haller, Violet Gray, Josh Graae, John Kealy, Mark McLean, and Keith Farnsworth.

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(Received 11 Jan 1994; revision accepted 15 Sep 1994)

APPENDIX A

Summary of the mapped distribution and management status of selected native, dominant species in California's Southwest Region. Statistics pertain to areas where the species was mapped as a canopy codominant (>20% of overstory cover), not the entire range of the species. Nomenclature follows the Jepson Manual. Geographic subregions include the Western Transverse Ranges (WT), South Coast (SC), San Gabriel Mountains (SG), San Bernardino Mountains (SB), San Jacinto Mountains (SJ), and Peninsular Range (PR). Land management status includes Level 1 (managed primarily for maintenance of biodiversity), Level 2 (public lands managed for multiple uses) and Level 3 (private lands not managed primarily for maintenance of biodiversity).

Species	Subregion (%)						Management level (%)			Area (sq. km)
	WT	SC	SG	SB	SJ	PR	L1	L2	L3	
Steppe Shrubs										
<i>Artemesia tridentata</i>	46	0	6	28	0	20	9	62	30	597
<i>Chrysothamnus nauseosus</i>	88	0	12	0	0	0	3	42	55	130
<i>Chrysothamnus parryi</i>	0	0	0	100	0	0	0	93	7	78
<i>Enneapterium farinosa</i>	3	89	0	0	1	7	7	17	77	97
<i>Ericameria linearifolia</i>	68	0	3	0	0	29	0	18	82	100
<i>Purshia glandulosa</i>	0	0	0	100	0	0	0	95	5	68
<i>Purshia tridentata</i>	82	0	0	0	0	18	0	56	44	38
Soft Chaparral Shrubs										
<i>Artemesia californica</i>	32	23	2	0	0	43	5	21	74	2548
<i>Encelia californica</i>	15	77	0	0	0	8	4	8	89	200
<i>Eriogonum fasciculatum</i>	31	20	5	2	0	43	7	31	62	3610
<i>Malosma laurina</i>	29	5	1	0	0	65	2	40	58	393
<i>Salvia apiana</i>	11	19	3	3	1	63	7	33	60	1200
<i>Salvia leucophylla</i>	99	1	0	0	0	0	7	6	87	853
<i>Salvia mellifera</i>	55	24	2	0	0	19	6	22	72	1188
<i>Yucca whipplei</i>	11	19	3	3	1	63	7	33	60	1200
Chaparral Shrubs										
<i>Adenostoma fasciculatum</i>	28	7	9	5	2	49	11	47	42	7969

APPENDIX A. CONTINUED.

Species	Subregion (%)					Management level (%)			Area (sq. km)
	WT	SC	SG	SB	SJ	PR	L1	L2	
<i>Adenostoma sparsifolium</i>	4	0	0	0	1	95	11	47	42
<i>Arctostaphylos glandulosa</i>	9	0	1	22	14	54	9	65	26
<i>Arctostaphylos glauca</i>	35	4	20	4	4	34	11	61	28
<i>Arctostaphylos parryana</i>	100	0	0	0	0	0	41	38	21
<i>Arctostaphylos patula</i>	5	0	6	86	1	2	38	52	10
<i>Arctostaphylos pringlei</i>	0	0	0	0	100	0	89	0	11
<i>Arctostaphylos pungens</i>	0	0	0	0	0	100	15	22	63
<i>Arctostaphylos tomentosa</i>	22	0	38	4	2	34	14	64	22
<i>Ceanothus cordatus</i>	11	0	15	66	9	0	52	39	9
<i>Ceanothus crassifolius</i>	25	9	25	6	0	35	18	46	36
<i>Ceanothus cuneatus</i>	0	79	0	0	0	4	27	17	55
<i>Ceanothus greggii</i>	8	1	6	15	10	61	14	60	25
<i>Ceanothus integrifolius</i>	0	0	41	59	0	0	36	40	24
<i>Ceanothus leucodermis</i>	7	0	28	13	6	47	18	60	23
<i>Ceanothus megacarpus</i>	95	2	0	0	0	3	17	24	59
<i>Ceanothus oliganthus</i>	19	1	28	0	0	52	20	50	30
<i>Ceanothus palmeri</i>	0	0	0	0	0	100	9	84	8
<i>Ceanothus sordidus</i>	0	9	0	0	0	91	0	38	62
<i>Ceanothus spinosus</i>	88	2	0	0	1	9	17	35	48
<i>Ceanothus tomentosus</i>	0	0	0	0	0	100	2	44	54
<i>Ceanothus verrucosus</i>	0	100	0	0	0	0	0	0	100
<i>Cercocarpus betuloides</i>	38	1	17	10	3	31	20	62	18
<i>Cercocarpus ledifolius</i>	0	0	20	18	0	62	7	86	7
<i>Chrysolepis sempervirens</i>	0	0	16	69	15	0	53	37	10
<i>Fraxinus dipetala</i>	0	0	0	0	0	100	0	88	13
<i>Fremontodendron californicum</i>	0	0	67	33	0	0	12	82	6

APPENDIX A. CONTINUED.

Species	Subregion (%)						Management level (%)			Area (sq. km)
	WT	SC	SG	SB	SJ	PR	L1	L2	L3	
<i>Heteromeles arbutifolia</i>	6	6	4	0	0	84	10	47	43	85
<i>Prunus ilicifolia</i>	88	1	12	0	0	0	3	69	28	132
<i>Quercus chrysolepis</i>	21	0	27	33	2	16	28	61	11	451
<i>Quercus dumosa</i> (per Munz)	39	2	12	10	1	36	16	54	29	4534
<i>Quercus wislizenii</i>	27	0	30	22	6	15	25	61	15	1422
<i>Rhus integrifolia</i>	33	16	15	0	0	35	11	29	60	470
<i>Rhus ovata</i>	0	1	17	8	0	74	22	32	46	263
<i>Syphocarpus mollis</i>	92	0	8	0	0	0	38	48	14	12
<i>Xylococcus bicolor</i>	0	6	0	0	0	94	3	39	57	219
Broadleaf Trees										
<i>Aesculus californica</i>	100	0	0	0	0	0	0	67	33	8
<i>Arbutus menziesii</i>	100	0	0	0	0	0	0	41	59	8
<i>Juglans californica</i>	60	9	0	0	0	31	3	8	89	60
<i>Quercus agrifolia</i>	22	4	1	1	1	72	8	30	62	728
<i>Quercus chrysolepis</i>	20	0	31	24	3	23	31	53	16	784
<i>Quercus douglasii</i>	100	0	0	0	0	0	0	0	33	6
<i>Quercus engelmannii</i>	0	0	0	0	0	100	3	32	65	236
<i>Quercus kelloggii</i>	2	0	5	31	7	55	9	50	41	457
<i>Quercus lobata</i>	100	1	0	0	0	0	2	7	91	50
<i>Quercus wislizenii</i>	0	0	100	0	0	0	0	100	0	53
Conifer Trees										
<i>Abies concolor</i>	13	0	17	52	9	9	31	52	17	788
<i>Calocedrus decurrens</i>	0	0	3	64	14	19	13	73	14	140
<i>Cupressus forbesii</i>	0	0	0	0	0	100	7	70	22	18
<i>Juniperus californica</i>	90	0	9	0	0	1	16	56	28	733

APPENDIX A. CONTINUED.

Species	Subregion (%)						Management level (%)			Area (sq. km)
	WT	SC	SG	SB	SJ	PR	L1	L2	L3	
<i>Juniperus occidentalis</i>	0	0	0	100	0	0	0	96	4	96
<i>Pinus attenuata</i>	0	0	42	59	0	0	0	90	10	15
<i>Pinus contorta</i>	0	0	14	79	7	0	83	14	3	59
<i>Pinus coulteri</i>	2	0	15	18	15	50	22	52	26	378
<i>Pinus flexilis</i>	0	0	1	88	11	0	91	9	0	45
<i>Pinus jeffreyi</i>	22	0	15	49	2	13	25	63	12	958
<i>Pinus lambertiana</i>	17	0	36	27	11	10	42	49	10	356
<i>Pinus monophylla</i>	73	0	6	20	0	1	14	73	13	1066
<i>Pinus ponderosa</i>	12	0	31	29	19	9	38	39	23	361
<i>Pinus sabiniana</i>	100	0	0	0	0	0	0	0	16	84
<i>Pseudotsuga macrocarpa</i>	25	0	43	24	0	9	35	54	11	43

APPENDIX B

Summary of the distribution and land ownership status of natural plant communities in California's Southwest Region. Communities are defined as in Holland (1986). Geographic subregions include the Western Transverse Ranges (WT), South Coast (SC), San Gabriel Mountains (SG), San Bernardino Mountains (SB), San Jacinto Mountains (SJ), and Peninsular Range (PR). Land management status includes Level 1 (managed primarily for maintenance of biodiversity), Level 2 (public lands managed for multiple uses) and Level 3 (private lands not managed primarily for maintenance of biodiversity). The mapped area for each community type is provided in square kilometers.

Community	Holland code	Subregion (%)						Management level (%)			Area (sq. km)
		WT	SC	SG	SB	SJ	PR	L1	L2	L3	
Scrub											
Coastal Scrub	32000	41	22	2	1	0	34	7	22	71	3908
Mojave Creosote Scrub	34100	0	0	73	0	27	33	39	28	86	86
Big Sagebrush Scrub	35210	46	0	3	26	0	26	3	59	38	334
Chaparral											
Northern Mixed Chaparral	37110	35	4	5	7	3	46	6	57	37	1143
Southern Mixed Chaparral	37120	1	10	0	0	0	89	3	35	62	219
Chamise Chaparral	37200	35	12	2	4	0	46	10	36	54	1407
Redshank Chaparral	37300	2	0	0	0	1	96	10	48	42	950
Semi-desert Chaparral	37400	5	0	8	8	9	70	18	59	24	1025
Mixed Montane Chaparral	37510	19	0	28	45	4	4	49	41	10	187
Montane Manzanita Chaparral	37520	0	0	0	0	0	100	5	58	37	13
Deer Brush Chaparral	37531	0	0	22	78	0	0	20	31	49	17
Whitethorn Chaparral	37532	7	0	26	2	0	64	11	62	28	337
Buck Brush Chaparral	37810	66	8	0	0	0	26	17	40	43	709
<i>Ceanothus crassifolius</i> Chaparral	37830	21	10	26	7	0	37	15	48	37	2045
<i>Ceanothus megacarpus</i> Chaparral	37840	96	2	0	0	0	2	18	25	57	572
Scrub Oak Chaparral	37900	32	1	14	10	1	41	22	56	23	1644
Interior Live Oak Chaparral	37A00	28	0	32	24	5	11	25	62	13	1174
Upper Sonoran Manzanita Chaparral	37B00	30	5	9	10	14	33	6	70	24	381

APPENDIX B. CONTINUED.

Community	Holland code	Subregion (%)						Management level (%)			Area (sq. km)
		WT	SC	SG	SB	SJ	PR	L1	L2	L3	
Southern North Slope Chaparral	37E00	66	0	12	11	0	12	55	44	1	14
Coastal Sage-Chaparral Scrub	37G00	7	27	4	0	0	61	1	17	82	64
Herbaceous											
Valley Needlegrass	42110	0	0	0	0	0	100	6	1	93	3
Non-native Grassland	42200	31	19	0	1	0	49	6	21	73	1165
Southern Coastal Salt Marsh	52120	0	82	0	0	0	0	28	14	57	13
Coastal Brackish Marsh	52200	0	100	0	0	0	0	0	0	100	1
Coastal/Valley Freshwater Marsh	52410	0	15	0	0	0	84	5	21	74	40
Riparian Woodland											
S. Coast Live Oak Riparian	61310	63	9	0	0	3	25	16	46	38	26
S. Arroyo Willow Riparian	61320	12	49	0	11	0	28	4	36	60	37
S. Cottonwood-Willow Riparian	61330	22	24	4	32	0	19	7	45	48	59
White Alder Riparian	61510	60	0	7	20	0	13	17	36	47	8
S. Sycamore-Alder Riparian	62400	14	1	0	0	0	85	7	28	65	17
Mule Fat Scrub	63310	31	57	0	0	0	13	5	35	60	45
Southern Willow Scrub	63320	0	100	0	0	0	0	0	12	88	1
Southern Alluvial Fan Scrub	63330	100	0	0	0	0	0	0	2	98	13
Broadleaved Woodland											
Valley Oak Woodland	71130	99	1	0	0	0	0	3	3	94	36
Blue Oak Woodland	71140	100	0	0	0	0	0	0	11	89	4
Interior Live Oak Woodland	71150	0	0	100	0	0	0	0	100	0	14
Coast Live Oak Woodland	71160	29	1	4	0	0	67	0	29	71	60

APPENDIX B. CONTINUED.

Community	Holland code	Subregion (%)					Management level (%)			Area (sq. km)
		WT	SC	SG	SB	SJ	PR	L1	L2	
Dense Engelmann Oak Woodland	71182	0	0	0	0	100	3	30	66	226
California Walnut Woodland	71210	57	10	0	0	33	3	8	89	56
Conifer Woodland										
Non-Serpentine Digger Pine-Chaparral	71322	100	0	0	0	0	0	0	100	4
Digger Pine-Oak Woodland	71410	100	0	0	0	0	0	24	76	9
Northern Juniper Woodland	72110	0	0	0	100	0	0	96	4	95
Mojavean Pinon Woodland	72210	0	0	66	34	0	0	94	6	62
Peninsular Pinon Woodland	72310	68	0	8	22	0	3	11	18	346
Peninsular Juniper Woodland/Scrub	72320	58	0	0	0	0	43	39	18	23
Cuyamian Pinyon Woodland	72500	87	0	10	4	0	0	14	62	939
Broadleaved Forest										
Mixed Evergreen Forest	81100	4	0	7	5	0	84	22	57	21
Coast Live Oak Forest	81310	45	8	0	0	0	46	8	22	70
Canyon Live Oak Forest	81320	32	0	27	11	10	21	37	49	14
Interior Live Oak Forest	81330	0	0	100	0	0	0	0	100	0
Black Oak Forest	81340	2	1	0	23	7	67	16	56	28
Conifer Forest										
Knobcone Pine Forest	83210	0	0	0	100	0	0	92	8	5
Southern Interior Cypress Forest	83330	0	0	0	0	100	7	70	22	17
Coulter Pine Forest	84140	3	0	19	21	8	49	14	59	27
Bigcone Spruce/Canyon Live Oak	84150	33	0	50	15	0	2	46	46	7
Westside Ponderosa Pine Forest	84210	14	0	28	34	16	8	44	35	21

APPENDIX B. CONTINUED.

Community	Holland code	Subregion (%)						Management level (%)			Area (sq. km)
		WT	SC	SG	SB	SJ	PR	L1	L2	L3	
Sierran Mixed Conifer Forest	84230	15	0	47	18	9	11	32	55	13	199
Sierran Pine Forest	85100	31	0	14	31	5	18	21	66	13	236
Jeffrey Pine-Fir Forest	85210	19	0	2	74	0	5	23	64	13	360
S. California White Fir Forest	85320	4	0	10	51	36	0	35	53	13	38
Lodgepole Pine Forest	86100	0	0	58	42	0	0	49	36	15	4
S. California Subalpine Forest	86500	0	0	3	81	16	0	92	8	0	52
Total		25	31	7	7	1	29	10	31	60	33832

NOTES

THE STATUS OF *CLARKIA MOSQUINII* (ONAGRACEAE).—L. D. Gottlieb, Section of Evolution & Ecology, University of California, Davis, CA 95616, and Lawrence Janeway, Herbarium, Department of Biological Sciences, California State University, Chico, CA 95929.

The species of *Clarkia* section *Myxocarpa* are closely similar morphologically and are often difficult to distinguish in the field. Geographical location is helpful with the six diploid species because they are distributed generally from north to south in northern California, from Shasta Lake to the central Sierra Nevada and, in any particular locality, one is unlikely to come upon more than two of them. However, the tetraploid *C. rhomboidea* ($n = 12$) is widely distributed throughout the same area and it may be confused with several of the diploids. The diploid species constitute an aneuploid series with the more northerly species *C. borealis*, *C. mildrediae* and *C. stellata* having $n = 7$, the centrally distributed *C. mosquinii* $n = 6$, and the species to the south *C. virgata* and *C. australis* $n = 5$.

The least known of the species in section *Myxocarpa* is *C. mosquinii* which was originally described as having two subspecies: subsp. *mosquinii* and subsp. *xerophila*, each from a single collection about 30 km apart in the Feather River region of Butte County (Small, Canadian Journal of Botany 49:1211–1217, 1971). The two subspecies were distinguished solely by a difference in leaf shape, with those of subsp. *mosquinii* said to be “elliptical to ovate” and those of subsp. *xerophila* “linear lanceolate” (Small, 1971). Because the type locality of subsp. *mosquinii* was not clearly identifiable from the type description (see below), and the type location of subsp. *xerophila* was inundated by the formation of Lake Oroville, it was not surprising that both taxa were listed as “Presumed Extinct” by Lewis (in Hickman, J. C., ed. The Jepson Manual, University of California Press, Berkeley, 1993).

Janeway (Madrone 40:268–269, 1993) reported a number of sites for subsp. *mosquinii* along Dark Canyon in Butte County, and three localities for subsp. *xerophila*, all in Butte County. Subsequent intensive field studies by Janeway (while in the employ of Plumas National Forest) located a number of additional sites. Janeway’s identifications were based entirely on morphological characters of plants growing at the sites. Consequently, to validate his identifications, we grew out plants from seeds collected at many of his sites, and examined their morphology and counted root tip chromosomes. Our results confirm that *C. mosquinii* is extant, but show, in conjunction with a careful reading of Mosquin (Ph.D. dissertation, University of California, Los Angeles, 1961) that the taxonomic recognition of subspecies is not warranted.

Root tip chromosome counts from freshly germinated seedlings grown from seeds along French Creek Road off of Oroville–Quincy Highway (Gottlieb 9310), French Creek at Road 34 (Gottlieb 9312), and Ponderosa Dam on the South Fork Feather River (Janeway 4582), all initially classified as subsp. *xerophila*, revealed $2n = 12$. This distinctive chromosome number proves that *C. mosquinii* is extant and grows at several sites in the region. Flowering material from each of these sites is represented by Janeway 4410 (CHSC, DAV), 4414 (CHSC, LA), and 4386 (CHSC), respectively. The Ponderosa Dam site was one of those previously reported by Janeway (1993). A second site reported in Janeway (1993), north of the French Creek Road crossing of Peavine Creek, was also confirmed in the field by Janeway in 1993.

However, root tip chromosome counts from Dark Canyon Road (Gottlieb 9320),

and three other morphologically similar collections from Butte County, Feather River Canyon at Bear Ranch Creek (Gottlieb 9318, 9319), Oroville-Quincy Highway south of Junction House (Gottlieb 9315), and Swayne Hill (Gottlieb 9314), revealed $2n = 24$, indicating the plants were actually *C. rhomboidea*, and suggesting that collections cited in Janeway (1993) as subsp. *mosquinii* are *C. rhomboidea*. Flowering material from these latter three sites is represented by Janeway 4364 (CHSC, CAS), 4399 (CHSC, LA, DAV), and 4366 (CHSC, DAV), respectively. Further field studies by Janeway in 1994 (again in the employ of Plumas National Forest), plus a reexamination of the specimens cited in Janeway (1993) confirms that the plants there reported are all *C. rhomboidea*. Compared to *C. rhomboidea*, *C. mosquinii* has a larger and protandrous flower with a relatively long style extending beyond the anthers whereas in *C. rhombidea* the stigma and anthers are at the same height and mature at the same time. In addition, the stem of *C. mosquinii* is erect 3–4 nodes above the highest open flower. In *C. rhomboidea*, the stem is generally recurved just above the uppermost flower. Surprisingly, a small number of *C. mosquinii* plants were found at Dark Canyon in late June, 1994; they had not been seen previously because they flower about four weeks later than *C. rhomboidea*.

Plants now referable to *C. mosquinii* were first collected by Mosquin (1961) as *C. virgata*, but with $n = 6$ rather than $n = 5$ characteristic of the more southerly *C. virgata*. Two collections were made and were described in his dissertation as follows: (1) Mosquin 3133 and 3335 from "Mayaro; 3.7 miles southwest of the entrance to Plumas National Forest, Plumas County," and (2) Mosquin 3336 from "Enterprise; 0.2 miles west of Enterprise along road to Oroville, Butte County."

Small (1971) designated Mosquin's collection 3335 as the type of *C. mosquinii* subsp. *mosquinii* and his own collection (Small 178) from the locality of Mosquin 3336 as the type of *C. mosquinii* subsp. *xerophila*, and noted that both taxa were known only from the type locations. His description of the type locality of subsp. *mosquinii* was that it was "along the California State Highway 40 Alternate, 3.7 miles southwest of entrance to Plumas National Forest." He did not include Mosquin's reference to Mayaro, a named site on Forest Service maps of the time, about 3 km northeast of Pulga on the Feather River Highway, now designated Highway 70, a lapse which proved unfortunate for later collectors. This was perhaps understandable since the specimen label did not include the reference to Mayaro. Thus, Janeway (1993) noted several unsuccessful searches by various botanists to relocate *C. mosquinii* subsp. *mosquinii*, and he presumed, in error, that the type locality was along Dark Canyon Road (formerly Highway 40 Alternate), which is indeed 3.7 miles (6 km) from the present Plumas National Forest entrance sign. However, the Mayaro site is about 13 km northeast of Dark Canyon, and also about 3 km northeast of Pulga which is cited in Lewis (1993) as the type location ("Feather River Canyon, near Pulga") of subsp. *mosquinii*. Mayaro and Pulga are both within what is commonly called the Feather River Canyon, but Dark Canyon is not.

Small (1971) distinguished the two subspecies of *C. mosquinii* only on the basis of presumed differences in leaf shape. Apparently he worked only from Mosquin's preserved material in describing subsp. *mosquinii*, and did not read Mosquin's dissertation which stated the variable nature of the character. "The two known populations of *C. virgata* ($n = 6$) are most variable with respect to leaf and petal shape. Most individuals of both populations have linear-lanceolate to lanceolate leaves, although other plants may have oblanceolate or ovate leaves" (Mosquin 1961, p. 14). Leaf shape was also variable on the plants we grew in the greenhouse.

We conclude that since the subspecies diagnosis depended only on differences in leaf shape and since this character is variable, there is no taxonomic basis to maintain subspecies within *Clarkia mosquinii*. The geographical distribution of *C. mosquinii*, as presently understood, includes the region between Mosquin's Mayaro site, near Pulga on the North Fork of the Feather River, south to Ponderosa Dam on the South Fork of the Feather River, a distance of about 30 km. Rediscovery of *C. mosquinii* is important because it provides a geographic and a phylogenetic link between the

northern species in section *Myxocarpa* with $n = 7$ and the southern species with $n = 5$.

(Received 13 Jul 1994; revision accepted 14 Sep 1994)

CUSHION-LIKE FRUTICOSE LICHENS AS *DUDLEYA* SEED TRAPS AND NURSERIES IN COASTAL COMMUNITIES.—Richard E. Riefner, Jr. and Peter A. Bowler, Museum of Systematic Biology and Department of Ecology and Evolutionary Biology, University of California, Irvine 92717.

The species-rich lichen communities of the coastal bluffs and cliffs in California and Baja California, Mexico, are able to survive because of the ability of lichens to readily absorb moisture from coastal fog. Similar situations are found in the diverse lichen floras of maritime zones in many other regions experiencing a Mediterranean climate (Nash et al., *Madroño*, 26:149–163, 1979). The often dense growth of fruticose lichens, particularly saxicolous *Niebla* species (Ramalinaceae), provides an interesting and unique micro-habitat. *Niebla ceruchoides* is a well known, easily recognized coastal saxicolous lichen occurring from northern Baja California, Mexico, to the San Francisco Bay region in northern California (Bowler et al., *Phytologia* 77:23–37, 1994). This species is identified readily by either its cushion-like fruticose thallus 1–2 cm high or a larger 3–4 cm high more open bush-like morphology. The cushion-like lichen mats resemble miniature wind-trimmed coastal sage scrub vascular plants, and the lichens are similarly sculpted to some extent by their exposure to wind and fog along the coastal rocks and cliffs. Both growth forms are gregarious and are characterized by dichotomously branched, terete laciniae that rarely exceed 1 mm in cross-section. *Niebla ceruchoides* is especially abundant in summer fog zones from Punta Banda to Morro Bay.

During an ongoing investigation of the relict endemic vegetation of summer fog zone habitats in the California Floristic Province by the senior author, observations of micro-habitats in which several *Dudleya* species occur indicate that an interesting association exists between a number of coastal, cliff-dwelling *Dudleya* taxa and *N. ceruchoides*. Apparently the dense, intricately branched thallus of this lichen effectively captures minute *Dudleya* seeds as they are dispersed in their seasonal seed rain across rock outcrops. The lichen cushion provides a foothold for the seedlings and possibly an enriched nutrient seed bed that encourages propagation of *Dudleya* seedlings on otherwise sheer rock. The resulting consolidation of soil allows additional humus accumulation and further plant colonization. The expanding *Dudleya* caudex fragments the lichen thallus and enhances dispersal of the lichen. This process is mutually beneficial by making additional lichen cushions available for colonization by *Dudleya*. Seed capture by the thallus may decrease the fortuitous dispersal of *Dudleya* seeds to unfavorable habitats, possibly contributing to the viability of several locally endemic *Dudleya* taxa. Other possible ways in which the micro-bushes of lichen could increase germination and recruitment success of *Dudleya* species include greatly increasing the presence of water available to the seedling due to fog capture (lichens are known to rapidly absorb moisture equal to 150%–1200% of their dry weight; Hawksworth and Hill, *The Lichen-forming Fungi*, 1984), and the protection of young plants from snail and slug herbivory. The cushions of lichen are particularly well suited for trapping soil particles that build a suitable substrate for vascular plant growth.

Large, reproductively viable populations of *D. stolonifera* in Orange County, *D. verityi* in Ventura County, *D. caespitosa* in San Luis Obispo County, and *D. anomala* and *D. campanulata* in Baja California Norte are consistently associated with exten-

sive populations of *N. ceruchoides*. *Niebla homalea*, a common saxicolous fruticose lichen, has broad flat or angular blades and a more open thallus, thus only occasionally acts as a seed trap. Seeds of annual grasses, such as *Muhlenbergia microsperma*, are also trapped and germinate in lichen cushions. Transplantation of the *Dudleya* seedling-lichen cushions may be useful in mitigation, restoration, and enhancement projects of coastal cliff and scrub habitats where other methods, such as rock-boring, have failed.

Fruticose lichen species of the saxicolous communities along the Pacific fog belt may enhance entrapment of intersystem nutrients such as atmospheric aerosols and occult precipitation that might otherwise escape deposition upon cliffs and outcrops in coastal ecosystems. The importance of the saxicolous lichen community, however, has been relatively unexplored in its role in mineral cycling and fog drip potential. Hypothetically, extensive mats of *Niebla* may influence the quantity and chemistry of precipitation throughfall in saxicolous habitats, thereby potentially affecting vascular plant abundance and diversity. Experiments are being designed by the authors to ascertain the importance of fruticose saxicolous lichen populations in nutrient cycling in the California Floristic Province.

The dense intricate branching of the fruticose *N. ceruchoides* in coastal communities may be especially effective in intercepting particulates, aerosols, and gleaning moisture and nutrients from fog. Munger et al. (Journal of Geophysical Research 88:5109–5121, 1983) report that fog water may contain greater concentrations of nutrients than precipitation. Specialized fog-trapping morphological adaptions are best known in the pendulous *Ramalina menziesii*, which has net-like reticulate fenestrations that effectively harvest moisture and nutrients from fog.

Azevedo and Morgan (Ecology 55:1135–1141, 1974) have identified summer fog as an important factor affecting water balances and nutrient cycling that in turn may influence species composition in coastal ecosystems. The capability of lichens to assimilate nutrients from rainwater, fog, particulates, and aerosols is well documented (Pike, Bryologist 81:247–257, 1978; Reiners and Olson, Oecologia 63:320–330, 1984; Lindberg et al., Science 231:141–145, 1986; Boucher and Nash, Botanical Gazette 151:114–118, 1990). The additional nutrients captured by these processes become available upon death and decomposition of the lichen or leached by precipitation and deposited on the surrounding soil/rock crevices. Corticolous lichens play a major role in nutrient cycling of numerous forest ecosystems. Knops et al. (Lichenologist 23:309–321, 1991) concluded that epiphytic lichens influence the amount and the chemistry of throughfall, and are important at the ecosystem level in capturing nutrients; saxicolous lichens may also prove to be as important in Pacific coastal communities.

We thank Gordan Marsh, Richard Ray, Connie Rutherford, John Trammer, and Carl Wishner for assistance with field work.

(Received 15 Mar 1994; revision accepted 16 Aug 1994)

NOTEWORTHY COLLECTIONS

ARIZONA

ECHINOCHLOA OPLISMENOIDES (Fourn.) Hitchc. (Poaceae).—Cochise Co., San Rafael Valley, along F.S. Rd. 227, T24S, R18E, S19, ne $\frac{1}{4}$ of ne $\frac{1}{4}$, elev. 1460 m, on wet margin of cattle tank in grassland with *Heteranthera* and *Marsilea*, 3 Oct 1993, *Mark Fishbein* 1512 (ARIZ), verified by John R. Reeder.

Previous knowledge. Known in México from southern Sonora and Chihuahua south to Estado de México and Puebla (R. McVaugh, Flora Novogaliciano, v. 14, 1983). The newly reported population is disjunct by 500 km to the northwest from the nearest documented populations in central Chihuahua, on the eastern slope of the Sierra Madre Occidental, at Cuautémoc and Majalca. In Sonora, this species has previously been reported from the Municipio de Alamos in the southeastern corner of the state (A. Beetle and D. Johnson, Gramineas de Sonora, 1991).

Significance. First record for United States. It is difficult to speculate whether the new record is the result of recent colonization or has been previously overlooked in a relatively poorly collected region of Arizona.

—MARK FISHBEIN, Herbarium and Department of Ecology and Evolutionary Biology, University of Arizona, Tucson 85721.

UTAH

OXYTROPIS RIPARIA Litv. (Fabaceae).—Tooele Co., vicinity of Grantsville, adventive in pasture after pipeline excavation, 1 Sept. 1993, *W. Bitner s.n.*, determined by M. Barkworth (UTC210399).

Previous knowledge. Native to eastern Europe, this oxytropis is known in the western U.S. from introductions in Montana, Wyoming, and southern Idaho, where it is sometimes grown as forage (R. Barneby in Intermountain Flora. V. 3 Part B, New York Botanical Garden, Bronx, 1989). The nearest documented occurrences include the Fort Hall (UTC197386, UTC198285, UTC198286, UTC199397) and American Falls Reservoir (UTC195553) vicinities in Bingham Co., Idaho.

Significance. First record in Utah, representing a distance approximately 250 km south of the Idaho collections.

LYTHRUM TRIBRACTEATUM Salzm. ex Spreng. (Lythraceae).—Cache Co., Cache Valley, south side of 600 South (the Mendon Road), 5.92 km west of Logan City limit and ca. 0.4 km east of the Little Bear River, 41°43'N, 111°56'W, elevation 1450 m, saline meadow on valley floor dominated by *Elymus smithii*, with *Distichlis spicata*, *Bromus japonicus*, *Poa pratensis*, *Hordeum jubatum*, *Phalaris arundinacea*, *Agrostis stolonifera*, and *Ammania robusta*, 10 Sept 1993, *M. E. Barkworth* 93-163 & *F. J. Smith*; duplicate verified by B. Erter and E. McClintock.

Previous knowledge. This southern European annual loosestrife is known from California (E. McClintock in The Jepson Manual, University of California Press, Berkeley, 1993) and southern Idaho in Gooding and Lincoln counties (UTC159386, UTC159347, UTC159364), but not from Nevada (J. T. Kartesz, A flora of Nevada, Ph.D. dissertation, University of Nevada, Reno, 1987).

Significance. First record in Utah, representing a distance approximately 240 km southeast of the Idaho collections.

—LINDA ALLEN, Intermountain Herbarium, Department of Biology, Utah State University, Logan, UT 84322-5305.

WASHINGTON

UTRICULARIA INFLATA Walter (Lentibulariaceae).—Cowlitz Co., Silver Lake, about 11 km E of Castle Rock, N side of State Hwy. 504 where it forms a causeway over the NE end of Silver Lake, T10N, R1W, sect. 26, elev. 150 m, 18 July 1994, L. Wilson s.n. (OSC); same locality, assoc. genera: *Nuphar*, *Potentilla*, *Typha*, *Menyanthes*, *Utricularia macrorhiza*, 17 August 1994, R. Halse 4826 (OSC, duplicates to be distributed).

Previous knowledge. This species is native to SE coastal plain from New Jersey to Florida, west to Kentucky and Texas; a sterile specimen from Horseshoe Lake, S of Port Orchard, Kitsap Co., WA (A. & E. Ceska 4913, K) has been reported by Taylor (The genus *Utricularia*, 1989, Kew Bulletin, Add. Ser. XIV, 1–724).

Significance. In Washington this extends the known range S about 124 km. In 1991, when this species was first observed, the plants were common over most of Silver Lake in emergent communities. The introduction of grass carp in 1992 to control aquatic macrophytes (*Myriophyllum*, *Elodea*) has also resulted in a dramatic decrease in the population of *Utricularia inflata*. The species is now primarily found in the NE corner of Silver Lake, in an area that is mechanically isolated from the rest of the lake and inaccessible to the grass carp. In 1994 the plants were in flower in July and August.

—RICHARD R. HALSE, Department of Botany & Plant Pathology, Oregon State University, Corvallis, OR 97331; LOVERNA WILSON, 1835 N.E. Steele Ave., Corvallis, OR 97330.

REVIEWS

Intermountain Flora. Vascular Plants of the Intermountain West, U.S.A. Volume 5. Asterales. By ARTHUR CRONQUIST. 1994. The New York Botanical Garden, Bronx, New York. 496 pp. \$75.00. ISBN 0-89327-375-9.

The publication of volume 5 represents another milestone in the Intermountain Flora project. This regional flora project was initiated in the 1940's and volume 1 was published in 1972. Since then additional volumes have appeared at irregular intervals and in an irregular sequence. To date, five volumes have been published: 1—*Geological and Botanical History, Plant Geography, Vascular Cryptogams, Gymnosperms, and Glossary* (1972); 6—*The Monocotyledons* (1977); 4—*The Asteridae Except the Asterales* (1984); 3, part B—*Fabales* (1989); and 5—*Asterales* (1994).

Volume 5 is the last major work of the late Arthur Cronquist, and represents well his impact on the floristics of North America. During his long and productive career, Art was a major contributor to regional floras of the Pacific Northwest, the northeastern U.S. and adjacent Canada, the southeastern U.S., and the Intermountain Region, and his influence extended to the floras of many other regions as well. At the time of his death, Art had read first proof on the text of volume 5, but less than half of the illustrations had been completed. Noel and Pat Holmgren, with the assistance of various collaborators, brought the book to completion.

As defined by Cronquist the Asterales consists of only one family, the Asteraceae. Art Cronquist's association with this family dates to early in his career, and *Erigeron*, the subject of his dissertation research, is the largest genus (72 species) of the Asteraceae in the Intermountain Region. Art had extensive field experience with the Asteraceae of the region and this is reflected throughout the volume in his comments on range, habitats, and patterns of variation.

Visually, the presentation of the Asteraceae is outstanding. The description of the family is clear and is followed by a brief discussion of the specialized terminology associated with the family. This discussion would have been enhanced by a plate in which the features were illustrated and contrasted. The book has an artificial key to genera, a synoptical key to tribes, and tribe by tribe keys to genera. For the Heliantheae there is a key to subtribes, and the genera are keyed within the subtribes. Descriptions and keys for species and infraspecific taxa are clearly written, but the descriptions often are not parallel in composition and information content. Some are of the "much like such and such but differing by thus and so" format. I much prefer descriptions that are fully parallel and comparable and that are written as a series of statements rather than one long sentence with a lot of semicolons. Full synonymy is presented with type citations. Common names are given for many taxa, though I noted that some widely used common names are omitted (e.g., sweet bush for *Bebbia juncea* and desert-chicory for *Rafinesquia neomexicana*). Each species is illustrated with one or more excellent line drawings. Habitat and range statements include both Intermountain and extralimital distributions. Descriptions are supplemented in various places with additional commentary.

Two new species and one new variety are published within the volume, and 32 new combinations are made. These are listed at the end of the taxonomic treatments. A short addendum by Noel H. Holmgren details several taxa that were described or documented from the Intermountain Region following Cronquist's death. The editors compiled name changes that appeared in the literature too late for Cronquist to have seen them and inserted them into the synonymy lists, but no changes were made in Cronquist's taxonomic treatments. The index includes both the recognized species and the synonyms.

I tried out the keys and found that in most cases they work well. In Group II of the artificial key, however, *Pectis papposa* keys to *Arnica*. Variable taxa often key in more than one place and exceptions are not shoehorned into places where they do not fit. The useful convention in which the key statement leading to a smaller number of taxa or subsequent couplets precedes the statement leading to a larger number is followed for the most part. The couplets are numbered, but the second of a pair of key statements is not distinguished by a prime. A parenthetical caveat beneath the title of the synoptical key to tribes warns that the artificial key should be used for identification. If one knows the tribe or can determine it from the key to tribes, an alternative to the artificial key is available.

The organization of the genera follows Cronquist's concept of tribal relationships. A few generic placements are questionable. Although acknowledging that *Rigiopappus* may be out of place in the Heliantheae subtribe Madiinae where it traditionally has been placed, Cronquist retained it there rather than including it in the Astereae. He also maintained the traditional association of *Raillardella* with *Arnica* rather than including the former in the Madiinae where recent evidence suggests it is better placed, but he did break from tradition in placing *Arnica* into the Heliantheae (as part of subtribe Arnicae) instead of the Senecioneae.

As treated by Cronquist and supplemented by Holmgren the Asteraceae of the Intermountain Region comprise 133 genera (not including some escapes from cultivation briefly noted in the addendum) and 616 species. By way of comparison the Asteraceae of California comprise 178 genera and 748 species (Hickman 1993). The comparison at the generic level is somewhat misleading, however, because of differing generic circumscriptions by Cronquist and some of the contributors to the *Jepson Manual*. If Cronquist had followed the generic concepts of the *Jepson Manual* authors, the genera of the Intermountain region would total 146.

Cronquist's generic concepts can best be represented by one word—TRADITION! Over and over Cronquist invoked his preference for traditional generic concepts in rejecting the contrasting views (and supporting evidence) of recent workers. As a result the Intermountain Region is still populated by numerous mismatched species of the dustbin genus *Haplopappus*. "*Haplopappus* is here taken in the broad sense that has been traditional (but disputed) since the monograph by H. M. Hall in 1928." *Eupatorium* too is maintained as a giant, polymorphic genus. "As traditionally (and here) defined, *Eupatorium* consists of nearly 1000 species . . ." It is not that Cronquist consistently preferred large, broadly inclusive genera. "*Kuhnia* has traditionally been held as a distinct genus, differing from the related genus *Brickellia* most notably by its plumose rather than merely barbellate pappus. . . . *Kuhnia* is a natural, readily recognizable group, nested in but easily distinguishable from *Brickellia*. In such cases I prefer to follow historical precedent." *Chrysopsis* (*sensu lato* including sect. *Phyllothecea*) and *Heterotheca* are kept separate despite the acknowledged facts that the pappus character that separates them occasionally fails and that some of their species are able to hybridize. After evaluating alternative treatments of these plants, Cronquist concluded ". . . I prefer to follow tradition." In total I noted seven instances in which Cronquist invoked tradition as his justification for making a taxonomic decision on generic limits.

In taking his stand on tradition, Art Cronquist rejected the work of many specialists who have used a variety of approaches to unraveling generic and species relationships. Among the taxonomists whose work was disregarded are Charles Heiser and Willard Yates (*Helimeris*), Harold Robinson and R. D. Brittell (*Rigiopappus*), Mark Bierner (*Dugaldia*), Gregory Brown (*Platyschkuhria*), Lowell Urbatsch (*Ericameria*), Ronald Hartman and Billie Turner (*Machaeranthera*), Thomas Watson (*Xylorhiza*), John Semple (*Heterotheca*), G. Ledyard Stebbins and Randall Bayer (*Antennaria*), Robert King and Harold Robinson (*Ageratina*, *Pleurocoronis*), and Spencer Tomb (*Lygodesmia*, *Prenanthes*).

Cronquist generally gave a brief discussion of the alternatives before taking his stand on tradition. Readers who wish to use alternative taxonomies can glean the

appropriate names from the synonymy lists. In one instance at the species level, however, I noted the absence of such commentary. Cronquist accepted *Baccharis glutinosa* Pers. and *B. viminea* DC. as distinct species and made no mention either of the study by Wilken (1972) that indicated that these names apply to seasonally dimorphic growth forms of the same species or the study by Cuatrecasas (1968) that indicates that *B. salicifolia* (Ruiz & Pavón) Pers. is the correct name for *B. glutinosa*, and hence for the species.

In a minority of cases Cronquist opted for a less traditional taxonomy. He followed Strother (1986) in part in dividing *Dyssodia* (*sensu lato*) into smaller genera. He accepted *Sphaeromeria* as distinct from *Tanacetum* and *Euthamia* as distinct from *Solidago*. Other examples are recognition of *Chloracantha* as a genus distinct from *Aster* and the inclusion of *Leucelene* within *Chaetopappa*.

In a way this is a review of more than just the Asteraceae of the Intermountain Region. Over his long career, Art Cronquist put his stamp on Asteraceae systematics over large parts of North America. In recent years Art established his concepts of traditional Asteraceae genera for the southeastern United States (Cronquist 1980), the northeastern U.S. and adjacent Canada (Gleason and Cronquist 1992), and now the Intermountain Region. In my opinion, a flora should reflect the state of taxonomic knowledge that existed at the time it was compiled. It is destined to become the standard reference for a region and its nomenclature infiltrates herbaria, classrooms, theses, journal articles, local floras, etc. Because the time between new regional floras is usually generational or longer, there is commonly a long time lag after a flora has been published before new advances in systematic knowledge become generally known. At the same time it is unavoidable that the taxonomic philosophy of the author or authors will be reflected in the pages of a flora. Cronquist's treatments of the Asteraceae of the Intermountain Region and other regions certainly are reflective of his conservative taxonomic philosophy. However, I do not believe that they reflect the current state of Asteraceae systematics. Too many recent advances have been rejected in deference to tradition. Preparation of generic treatments for the Asteraceae of North America will soon be undertaken as a part of the *Flora of North America* project. I hope that the taxonomic decisions that are made for FNA are based on the best data available and not on tradition.

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—DAVID J. KEIL, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

Ethnobotany of the California Indians. Volumes 1 and 2. By B. M. BECK and S. S. STRIKE. 1994. Illustrations by E. D. Roeder. Koeltz Scientific Books, Champaign, Illinois. Vol. 1—165 p.; Vol. 2—210 p. \$80.00.

The new two-volume series on the ethnobotany of the California Indians is a welcomed compendium of aboriginal uses of California plants. Volume 1 is a bibliography and index compiled by Beatrice M. Beck of the Rancho Santa Ana Botanic Garden. It originated as a smaller bibliography for a class sponsored by the Rancho Santa Ana Botanic Garden. Volume 2 is a compendium of the aboriginal uses of California's indigenous plants written by Sandra Strike, also affiliated with the Rancho Santa Ana Botanic Garden.

Beck has gathered an extensive, apparently exhaustive, collection of references from a host of published and "gray" sources. I was pleased to see such an extensive literature on the ethnobotany of California that includes botanical, anthropological, and ethnobotanical entries. Many of the references were familiar to me, but a greater number were not. What I found most useful in Volume One was the name of the plant(s), general use, or aboriginal group discussed in the reference, listed after each citation, when relevant. The plant listing is either a colloquial or Latin name, presumably reflecting the usage in the citation. One must presume that all plants discussed in each reference were listed after the citation.

Somewhat troublesome, however, was a lack of consistency in the listing of plant names and the inaccuracies of the index seen throughout the volume. *Acacia*, for example, is listed as appearing on page 13, but it appears on page 14. *Calochortus* is listed as appearing on pages 13 and 114. It appears on pages 14 and 114. However, the common name for *Calochortus*, "mariposa lily," is cited as appearing only on page 13 (it does not). Although I presume the plant citations reflect the names as used in the reference, the lack of consistency in referencing, cross-referencing, and citations for both Latin and common names seriously diminishes the volume's utility for scientific research.

In addition, many of the Latin names are misspelled (e.g., *Martyniaceae* as *Martyniacea*, *Adenostoma fasciculatum* as *A. fasciculum*). Nomenclature is not completely faithful to the *Jepson Manual*. The index lists *Sequoia gigantea*, not *Sequoiadendron giganteum*, for example. Also peculiar were taxa of which I have no knowledge, and for which I could find no references in our standard botanical texts. For example, I am not familiar with *Scirpus lacustris* (found on page 161 of the index, and cited as occurring in Robert Heiser's 1937 article in *American Antiquities*). I could not find *S. lacustris* in the synonymy of the new *Jepson Manual*; there is no mention of *Scirpus lacustris* in Volume 2. In short, considerable sleuthing is needed to determine to which *Scirpus* Heiser was referring. Although some botanists have access to the necessary botanical references to solve the mystery, I suspect the average user, particularly the non-botanist/anthropologist, will not. This difficulty was not peculiar to *Scirpus*; I went down the "S's" in the index and found the same problem with *Sambucus glauca*. Most of us won't know whether these represent old names or misidentifications. One final irritation with the index is that Latin names are not italicized—a practice that makes finding a scientific plant name much easier as it stands out against all the other entries in an index.

Volume 2, *Aboriginal uses of California's indigenous plants*, is organized alphabetically by genus. Major plant uses are indicated by one or several of five symbols representing food (F), medicine (M), basketry (B), dye (D), and the catchall "other" (O). I found these classifications somewhat traditional, unimaginative, and disappointingly limiting. Many "other" uses are as distinctive as dyes or basketry, and I see no reason, given the detail of the catalogue, why additional use categories such as ritual items, housing materials, etc. could not have been delimited. While I have enjoyed very much perusing this catalogue of uses, and have learned many new things, I would have organized this volume quite differently. For example, uses for each plant are listed individually without the specific citation, so one has no way of knowing

the primary reference. This feature, again, limits the utility of the volumes for original scientific research.

Some oddities in the volumes' production also were apparent. For example, both Volumes 1 and 2 have a bibliography (Volume 1 is a bibliography), but references in the much shorter bibliography of Volume 2 do not all appear in Volume 1. Others are not thoroughly cited. For example, Elsie Allen's work on Pomo basketmaking published by Naturegraph Publishers, Inc., is cited as the revised edition (1988) in Volume 2, but as the original, published in 1972, in Volume 1. I do not understand why, if these volumes represent a pair in which one is indispensable without the other, why the bibliographies are not combined. The illustrations by Emily Roeder are reasonable, but do not compare to those produced by the superb artists, such as Dr. L. Vorobik and E. Reid, who contributed to the *Jepson Manual*. To make more of an impact and thus enhance Volume 2, more illustrations would have been essential.

Overall, Beck and Strike have provided us with an indispensable compendium of aboriginal uses of our California plants, but due to the serious and unnecessary shortcomings mentioned in this review, the two volumes are not as immediately useful nor accessible as they could have been. In short, given the somewhat sloppiness of the preparation of the volumes, their limited utility in original research, and their clearly unreasonable cost (\$80.00), it would not be responsible to urge students of California ethnobotany to purchase this pair. Rather, I would suggest that they would be incorporated into libraries and herbaria as a much needed, even essential, accounting of our state's ethnobotanical history.

—PEGGY L. FIEDLER, Department of Biology, San Francisco State University, San Francisco, CA 94132.

Conservation Biology: The Theory and Practice of Nature Conservation, Preservation, and Management. By P. L. FIEDLER and S. K. JAIN (eds.). 1992. Chapman and Hall, New York. xviii + 507 pages. ISBN 0-412-01951-5 (hb), 0-412-01961-2 (pb).

This collection of papers and essays, which addresses important issues in theory and application of conservation biology, arrived a year ahead of the current wave of textbooks on the topic. The book grew out of a graduate seminar series organized by the senior author at San Francisco State University in 1988. It does exactly what such an effort should do, that is, it provides a sampling of current concerns and efforts in the ever-expanding field of conservation biology.

The book is organized into four sections, with a foreword (by John Harper), and an epilogue by the editors. Each section containing several empirical or theoretical chapters and one or two essays. The first section, "The Natural Order", contains several chapters that provide overviews of species richness patterns, causes of natural rarity, and genetic conservation in agroecosystems.

The second section discusses processes and effects of ecological change, and includes chapters on reptilian extinctions, fish biodiversity, invertebrate conservation, and forest fragmentation. As a whole, these papers provide both a historical perspective on community change and indications of causes of biodiversity decline. The compilation of data on threats to invertebrate diversity by Haferink was especially useful and novel. The chapter by Harris and Silva-Lopez includes many definitions and clarifications of the effects of habitat fragmentation on biodiversity.

This section is followed by one dealing with the biology of small populations. It includes chapters dealing with genetics, demography, and social behavior, all important issues that must be integrated in predicting the behavior of small populations. Pearl's chapter on behavioral aspects of the ecology of Asian primates was especially illuminating as regards the complexity involved in conservation of social animals.

Her suggestions for needed avenues of research should inspire studies on these and other social animals. An essay by Guerrant provides an overview of genetic and demographic considerations for sampling and reintroduction of rare plants, and provides a list of important considerations for anyone planning a research project on an endangered or threatened plant, or to those engaged in a restoration project.

The final section of the volume turns practical, with chapters on management of preserves and on ex situ conservation. It deals with issues such as active management of very sensitive natural areas (Carroll), and the role of botanical gardens in the conservation of plant species (Falk). Particularly noteworthy in this section is a theme touched upon by all the authors: that successful conservation strategies require a many-tiered, proactive approach.

This book is most useful for graduate seminars in conservation biology. It has been superseded as a general conservation biology text by several other recent books. It remains, however, a critical assessment of specific problems in conservation biology. As such, the uneven nature of the science is reflected in the varying depth of coverage across the chapters. The origin of the book as an aggregation of individual seminars rather than a comprehensive manuscript, delivers only the contributing authors' slices of a very large field. Nevertheless, this shortcoming will ultimately sustain the book's use. Students will find value in the case histories and specific information in this book long after the latest principles of conservation biology (and their textbooks) have been shed.

—BETH BRAKER, Department of Biology, Occidental College, Los Angeles, CA 90041, and TOM SCOTT, Department of Earth Sciences, University of California, Riverside, CA 92521.

Ed. Note. A 2nd edition, greatly revised and expanded, is due to appear in 1996.

ANNOUNCEMENT

RANCHO SANTA ANA BOTANIC GARDEN
11TH ANNUAL SOUTHWESTERN BOTANICAL SYSTEMATICS SYMPOSIUM
THE NEW MORPHOLOGY: INTEGRATIVE APPROACHES
MAY 26 & 27, 1995

Rancho Santa Ana Botanic Garden at Claremont is pleased to present its 11th Annual Botanical Systematics Symposium on May 27, 1995. The topic will be "The New Morphology: Integrative Approaches." The keynote speaker is **Elliot M. Meyerowitz**, California Institute of Technology, discussing "Models for the Developmental Origin of Patterns in Flowers." Papers will be presented by **John F. Doebley**, University of Minnesota ("Genetic Analysis of the Morphological Evolution of Maize"), **Carolyn Napoli**, University of California at Davis ("Genetic Analysis of Meristem Organization and Identity in Petunia"), **Mark Running**, California Institute of Technology ("Using Confocal Laser Scanning Microscopy in the Study of Plant Structure and Development"), **Cynthia Jones**, University of Connecticut ("The Concept of Bauplan and its Relevance to Interpretation of Diversity in Seedling Structure in *Pelargonium*"), **Geeta Bharathan**, University of California at Davis ("Phylogenetic Approach to the Evolution of Leaf Development in Monocotyledons"), and **Rob DeSalle**, The American Museum of Natural History ("Insect Model Systems for Studying the Interface between Developmental Genetics and Evolution").

The cost to attend this symposium is \$60.00 per participant (\$45.00 for students). This fee includes the Friday evening social, boxed lunch dinner on Saturday. To register please send your name, address and telephone number along with a check payable to:

Rancho Santa Ana Botanic Garden
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Be sure to register early as space is limited. For more information, please call Ann Joslin (909) 625-8767, ext. 251, or e-mail to joslina@cgs.vax.claremont.edu.

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CALIFORNIA BOTANICAL SOCIETY

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SPECIAL ISSUE: THE FUTURE OF CALIFORNIA FLORISTICS AND SYSTEMATICS: RESEARCH, EDUCATION, CONSERVATION

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MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$50 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to the treasurer.

Editor—ROBERT PATTERSON
Department of Biology
San Francisco State University
San Francisco, CA 94132

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THE FUTURE OF CALIFORNIA
FLORISTICS AND SYSTEMATICS:
RESEARCH, EDUCATION, CONSERVATION

Proceedings of a Symposium Sponsored by the
Friends of the Jepson Herbarium
June 3, 4, & 5, 1994

All papers in this issue of *Madroño* are derived from a symposium held in the new quarters of the Jepson Herbarium, within the renovated Valley Life Sciences Building, University of California, Berkeley. The purpose of the symposium was to facilitate communication among academics, professional botanists, and interested amateurs, and to explore future roles for the Jepson Herbarium in enhancing such connections through its research and educational programs. The published versions of talks and workshops that follow are enhanced by the peer review process and modified to some extent by discussions at the symposium itself, but fairly represent the spectrum of approaches taken to address these goals and are meant to retain some of the informal flavor of the presentations themselves.

Over 250 enthusiastic people attended the weekend appropriately dubbed a “botanical Woodstock” by Peter Raven. A reception was held Friday night, with guided tours of the new JEPS/UC herbaria space and a profusely illustrated and educational talk by Lincoln Constance on the “History of Berkeley Botany and the Jepson Herbarium.” On Saturday morning, Robert Ornduff presided over a plenary session that included talks by Brent Mishler (“The Future of Plant Systematics, Science, and Society”), Dieter Wilken (“Flowers in the Garden: What Next for California Floristics?”), Barbara Ertter (“The Changing Face of California Botany”), George Rogers (“Cooperation and Collaboration: Herbaria and Botanical Gardens”), Peggy Fiedler (“Rarity in California Plants: New Thoughts on Old Ideas”), and Bruce Baldwin (“The Jepson Herbarium: Designs for the Future”).

The afternoon was taken up with several concurrent workshops: “Threats to the California Flora” (panel: Rowan Rountree, Elizabeth Painter, Jon Keeley, Kristina Schierenbeck, Oren Pollak, Roxanne Bittman), “Collecting Guidelines and Documentation Techniques” (panel: Wayne Ferren, Teresa Sholars, David Magney), “California’s Fabulous Flora: Partnership in Study and Conservation of a Declining Treasure” (Mark Skinner), “How To Use The Jepson Manual” (Elizabeth Chase Neese, Ellen Dean), “The Use of

California Native Plants in the Landscape" (panel: Warren Roberts, Roger Raiche, Mike Evans, Barbara Coe, Frank Chan, Carol Bornstein, Ron Lutsko, Nevin Smith), "Botanical Transect: Bodega Bay to Vacaville" (G. Ledyard Stebbins), "The Future of California's Floristic Heritage on Public Lands" (panel: Ken Berg, Sandy Morey, Sarah Allen, Jan Knight, Jim Shevock, John Willoughby), and "Biodiversity Information Management" (panel: Thomas Duncan, Chris Meacham, Natalie Munn, Susan Stone). In the evening, following a magnificent banquet (with wine bearing the *Jepson* label), Peter Raven presented his keynote address on: "The University, the State, and the Loss of Plant Biodiversity Around the World" to a packed house of attendees and members of the press.

A number of field trips, led by local experts, were successfully held on Sunday to: UC Botanical Garden (Robert Ornduff), Ring Mountain (Phyllis Ellman), Mt. Tamalpais (Wilma Follette), Pt. Reyes (Virginia Norris and Margriet Wetherwax), East Bay localities (Barbara Ertter), and Ledyard Stebbins' Transect (a two day trip, Bodega Bay to Vacaville; co-led by Fred Hrusa).

The Jepson Herbarium has long been a leader in developing tools by which the California flora may be better understood, and it will continue to strive for understanding of the complex California flora through systematic and evolutionary studies. This symposium will be instrumental in more clearly defining future efforts of the Jepson Herbarium in other arenas as well: educational programs at several levels ranging from the general public, to amateur botanists, to professional consultants, to agency and organizational staff, to undergraduate and graduate students, combined with an enhanced role as liaison between these groups. It is abundantly clear that only through cooperation of and communication among all interested groups will we be able to fully understand and protect our native plants.

ACKNOWLEDGMENTS

We thank many people who helped put on the symposium: Irene Acosta, Tom Atherstone, Elly Bade, Daniel Campbell, Karen Carkhuff, Katherine Culligan, Derek Maskell, Shirley McPheeters, Jerry Parsons, Gorgette Salazar, Fosiee Tahbaz, Linda Vorobik, Roy West, Karen Wetherell, Margriet Wetherwax, Myrtle Wolf, and many others who assisted. We also appreciate the labors of Madroño Editor Robert Patterson in helping to turn the talks into polished manuscripts.

DEDICATION

We dedicate this symposium to the memories of Dr. Lawrence R. Heckard and Dr. James C. Hickman, who were so instrumental in the recent accomplishments of the Jepson Herbarium. Dr. Heckard's outstanding research on the systematics of Scrophulariaceae subtribe Castillejiniae and his leadership in rare plant conservation efforts with the California Native Plant Society were two hallmarks of his distinguished career as Curator of the Jepson Herbarium. Dr. Heckard's influence will continue to be felt at the Jepson Herbarium, in indirect and direct ways, such as his bequeathal

of the Heckard Fund for research on the California flora. Dr. Hickman and Dr. Heckard, while engaging in floristic research on Snow Mountain, conceived the idea of an entirely new *Jepson Manual* of California plants. Together, they were the primary force in making that dream a reality. Dr. Hickman's guidance as editor of the *Jepson Manual* was instrumental to timely completion of the project. We owe both Dr. Heckard and Dr. Hickman a huge debt of gratitude for their efforts.

—BRENT D. MISHLER, BRUCE G. BALDWIN, and SUSAN D'ALCAMO, Jepson Herbarium, University of California, Berkeley, 94720-2465

(Received 7 Oct 1994; accepted 3 Feb 1995)

HOMAGE TO WILLIS LINN JEPSON

LINCOLN CONSTANCE

University Herbarium, and Department of Integrative Biology,
University of California, Berkeley, CA 94720

Willis Linn Jepson was, I believe, the first California-born botanist. Certainly he was the first one of consequence. His parents, William L. and Martha Ann Jepson, left Missouri on the Overland Trail in 1857 as part of a train of three ox-drawn wagons, crossed the plains and mountains without serious incident, and settled on a farm in Vacaville Township, Solano County, California. There six children were born; Willis Linn, the first of two boys, was born in 1867. He always referred to his childhood home in the rolling hills on the edge of the Great Valley as a virtual Eden. Thus he wrote in 1912: "In early days these plains and valleys were in the springtime a wonderful natural garden, literally with a hundred flowers to the square foot, the whole in riotous abundance and running out across the low hills in streamers of yellow and blue . . . It was a rich inheritance for a child to have been born in such a wild garden and to grow into a lad with the flowers rioting each springtime over his head, making for him a hundred ways and a thousand tempting fairy places, all aglow with color, all distinctive with delicate structures, all alive with curious interest." And again, 33 years later, a year before his death: "The blue oaks, every one, on every slope glow radiantly in their new foliage—almost a touch of gold in the swelling crowns. Along the slopes there is now an exhalation of light, of cheer, of animation—as if all the groves joined in a happy and lightsome dance: The winter is past! The winter is past! In the hollows and at the heads of cañons the colonies of Buckeye in their intensest green set off by contrast the gayety of the hills, while a few great trees of the Valley Oak, sequestered on the ridges, stretch dark limbs to the sky, their dignity as yet undisturbed by the warm zephyrs which unlocked the gaunt arms of their cousins. But what a scene now lies in the sparkling sunlight! In that little range of hills all is primitive . . . So, on such green slopes, on such an unspoiled woodland, new born in the spring sunlight, let elves and goblins play! This light and airy immanence of the hills, the blue oaks in the freshness of new leaf, lasts only a week, but in that one week are stirred the gayest and happiest moods of nature's self in the Araquipas. And then it is all gone and one must wait a whole year for its recurrence."

In such a setting and with strong maternal encouragement, it is not surprising that he developed an almost religious life-long devotion to natural history. A career-determining incident in "the early eighties" may have been a trip he made alone to the California Academy of Sciences in San Francisco, where he was befriended by Edward Lee Greene and also had the pleasure of meeting the aging Albert Kellogg, one of the Academy's founders.

Greene was the first strictly botanical appointee to the University of California. His designation as Instructor in 1890 in the new College of Natural Sciences marked the official founding of a Department of Botany. He was at the same time Rector of St. Mark's Episcopal Church; apparently no conflict between religion and science was perceived. Jepson wrote to Joseph Grinnell many years later: "I was appointed Assistant in the Department of Botany the day of its foundation in 1890. The Department consisted of a large room in South Hall, a low partition partially shutting off a sanctum for the Professor of Botany. In one room was everything: laboratory; lectures; the herbarium; mounting for the herbarium; drying of plants; office of the botanical garden; botanical museum; library room, and so on." He became one of a group that included Marshall Avery Howe, Ivar Tidestrom, and Joseph Burtt-Davy. This seems to have been a congenial club who admired their professor, maintained strong ties, and corresponded actively for many years.

As has repeatedly been stated, Greene was a controversial figure. Jepson described his personality as "many sided, highly interesting, in many ways remarkable, and often singularly puzzling . . . it may well be that a just appraisement of his work must wait on the years." He admired Greene's independence and his classical scholarship; some of the older man's interest in botanical history rubbed off on his students. But Jepson sharply diverged from Greene's Special Creationism and his rejection of Darwinian evolution. I have found no correspondence between the two after the publication of Jepson's doctoral thesis, "A Flora of Western Middle California" in 1901. Kate Brandegee chimed in with the observation (referring to Greene): "I think he's not sane. Did he ever tell you that his father spent the last dozen years of his life in an insane asylum and died there? His affliction took the form which the French call 'the insanity of grandeur.' "

In co-founding the journal ERYTHEA with his star pupil, Greene afforded Jepson an important platform to make himself widely known and respected throughout the botanical community. B. L. Robinson of Harvard wrote the new editor: "I am also very glad to hear of your plan of working over Prof. Greene's species. You can scarcely do a better piece of work for American systematic botany than to make a critical and dispassionate study of his species . . . I do not think your task will be an easy one but it will not be thankless either.



A. As a boy.



C. 1897, Ukiah, California.



B. 1896.



E. 1928, in his office at UC Berkeley.



D. 1911, in the Sierra Nevada.

FIG. 1. Willis Linn Jepson. Photos courtesy of the Jepson Herbarium.

There will be a number of us who will sincerely appreciate your efforts in the cause of accurate science."

When Greene left Berkeley in 1895 to accept a position at the Catholic University of America, the event was heralded by The San Francisco Call as "Berkeley's Great Loss." There was much discussion as to whether and how Greene should be replaced, or whether Dean Hilgard should be allowed to absorb Botany into the College of Agriculture, with or without a new appointment. Hilgard's candidate was Charles E. Bessey, whose New Botany was attracting considerable attention at the time. Just in case Hilgard succeeded, Jepson applied to the Oregon Agricultural College in Corvallis, albeit unsuccessfully. Some observers thought it would be logical that Jepson should succeed Greene since "he is the most promising young botanist in the country and the most effective worker on the Pacific Coast." But Jepson was not to receive the doctorate (the first one given in Botany in the University) for another three years, and the regents had insufficient funds to attract Bessey. So, they compromised: William A. Setchell, with Yale and Harvard degrees and expertise in algae and fungi—part of Bessey's New Botany, was awarded the position. So technically, Jepson received his Ph.D. under Setchell, who was only three years his senior. Factually, he was largely self-educated with important input from Greene and some additional burnishing acquired through half-years spent at Cornell and Harvard, respectively. Just why the early warm friendship between Setchell and Jepson turned into active rivalry and eventually froze into animosity will doubtless continue to be a subject of speculation. The marked differences between these two strongly independent personalities were probably sufficient to bring about that result. At all events, it was a matter of real concern to graduate students of the twenties and thirties. Jepson worked his way slowly but steadily through the academic maze for the next 46 years, culminating in emeritus status in 1937. Like Greene before him, he complained bitterly that academic advancement was slow in coming, doubtless a factor in his progressive disillusionment with university administration in general.

In 1900, he discontinued publication of *ERYTHEA* to the expressed regret of many subscribers (including Bessey), to concentrate on his floristic investigations. His ultimate goal, conceived even before he entered Berkeley, was to produce a flora of California that would treat all the vascular plants of the state at an almost monographic level. The project was based on the assumption that one individual could hope to know a flora of several thousand taxa in that degree of detail. The first fascicle appeared in 1909, the last in 1943, but its completion was thwarted by age and undefined illness, the latter having haunted him all his life. Along the way he found time to expand his thesis/flora into the much admired "Manual of

the Flowering Plants of California," certainly his most widely used and influential book. There also were remunerative high school texts. He created the California Botanical Society and founded and for many years edited its journal, MADROÑO. His "Silva of California" is a handsome coffee-table example of its author's dedication to forestry and forest conservation. The University presented a specially bound copy to President Theodore Roosevelt when he visited the Berkeley campus on Charter Day in 1911. Among the students he trained or strongly influenced were: Harvey M. Hall, Helen M. Gilkey, Alice M. Ottley, David D. Keck, John Thomas Howell, Herbert L. Mason, Lauramay Dempster, J. Edison Adams, Mary L. Bowerman, Joseph Ewan, Robert F. Hoover, and myself. I came to know him only in his mid-sixties, when he was past his physical prime, but perhaps at the height of his mental powers. He was so engrossed in his Flora by that time that he had erected a protective secretarial screen to protect himself from unnecessary human contact, but he could be warm and hospitable if one could get beyond the barrier. But the passage was not easy and the outcome was unpredictable. He no longer made a pretense of lecturing to his classes—they were turned over to his associate, Herbert Mason, but he still did conduct a weekly seminar, and he could be an effective teacher on an individual basis.

Jepson was elected Faculty Research Lecturer for 1934, the highest honor the Faculty Academic Senate can bestow upon one of its members. His subject was "The content and origin of the Californian flora: A demonstration of scientific methods." I attended it and remember that it dealt successfully with problems of natural variation influenced by environmental factors drawn from the California poppy and other "difficult" groups. He enjoyed the adulation he received, and his students were suitably impressed. In June of the same year, Setchell retired and stepped down as departmental chairman after 39 years.

The university administration decided that this would be a propitious opportunity to re-examine this small and distinguished, if sometimes raucous department. The conclusion was reached that Plant Science on the Berkeley campus would be best served by augmenting the botany staff with faculty members drawn from several areas of the College of Agriculture. The plan was implemented by appointing a new chairman from the Division of Plant Nutrition. Jepson found this procedure doubly intolerable—to pass over the departmental faculty, of whom he was clearly the senior member, and to infuse the department with faculty from the College of Agriculture! Although he came to like, or at least tolerate, some among the Agriculture personnel—particularly Alva R. Davis, he regarded this action as the ultimate treachery. The administration, on the

other hand, did not dare offer him the chairmanship, even if it had been disposed to do so, for fear he would accept the invitation.

The California Botanical Society celebrated its silver jubilee (25th anniversary) on 23 April 1938. Jepson gave the principal address, a retrospective of the society and much else. This was published in volume 4 of *MADROÑO*, which was appropriately dedicated to the founder. In 1941, Jepson was awarded an LL.D. Pictures show him at the ceremony, tall and erect and clad in this cap and gown, in the Greek Theater, in rituals presided over by President Robert Gordon Sproul and by Charles B. Lipman, Dean of the Graduate Division, his arch enemy. The last installment Jepson contributed to the Flora of California, terminating in the genus *Solanum*, with the formidable prospect of Scrophulariaceae confronting the author, was issued in 1943. His final years were dogged by ill health and especially bitter frustration at knowing that there was no way he could ever complete the great Flora.

The whole thrust of Jepson's research and teaching was the unified objective of reaching a better understanding of the plant world of California and transmitting that knowledge by both written and spoken word to as wide and diverse an audience as possible. A strong sense of the dramatic and a carefully cultivated lyric expression were important instruments in this process. The "field,"—the environment—was almost as important as the flora itself. He never became much interested in the niceties of nomenclature, although he made a point of attending all international botanical congresses and participating in their nomenclatural sessions. He elected to follow a relatively conservative pattern, in contrast to Greene's extreme practices. His taxonomic emphasis was on careful observation and description of plants as they grow in nature, and on meticulous documentation. In a fit of desperation occasioned by discovery of serious insect damage in his herbarium, he commented: "The herbarium will be my monument, more than the flora. Eventually the flora will be, in a way, out of date. The herbarium never will be—botanists will always wish to go back to it." The encouragement of amateurs was an important part of his overall program. He attracted them by lectures and popular articles, and his usually careful attention to requests for identifications and information. He had willing contributors in every corner of the state, several of them of expert status.

He was not afraid of innovation, but he did look at vaunted taxonomic improvements with a critical eye. He knew about cytogenetics and chromosome number, which came into vogue in his later years, but probably wisely concluded to stay with familiar techniques. I don't think he would have been abashed by electronic methods and information based on DNA, although he might have regarded them as the telomes and flavonoids of this era. Critical

observation, careful documentation, and lucid expression were the essence of his teaching.

In my opinion, Jepson laid a solid foundation for the continued and expanded investigation of the California flora, by whatever means, well into the 21st century. For this, we honor him tonight.

(Received 15 Aug 1994; accepted 9 Sep 1994)

PLANT SYSTEMATICS AND CONSERVATION: SCIENCE AND SOCIETY

BRENT D. MISHLER

Jepson Herbarium, University Herbarium, and
Department of Integrative Biology, University of California,
Berkeley, CA 94720-2465

ABSTRACT

Systematics is the preeminent science of biodiversity. Differences among species, and among natural phylogenetic groupings of species, represent the major legacy of biological diversification on earth. Pressures of development are causing an alarming increase in the rate of species extinction; intelligent decisions concerning the use or preservation of any species hinge on the existence of a fundamental understanding of species boundaries, species origins, and species relationships, making a renaissance in systematics especially timely. Newly developed methods for data gathering and analysis of phylogenetic relationships (i.e., the genealogy of species) position us on the threshold of a deep understanding of the history of the biological world, but too few systematists are being educated to meet the increased demands for phylogenetic research and its integration into conservation biology. We must break down the widely perceived (but false) barrier between "academic" phylogenetic systematic studies and "applied" studies of floristics and plant conservation; species preservation efforts that are carefully focused and justified by phylogenetic criteria will receive much greater public support. Because of its unusual combination of attributes, with large herbaria and botanical garden as well as a number of supporting laboratories located within a major research university, the University of California at Berkeley can make a unique contribution within California (and indeed the western United States) to this process of integration of systematics and conservation through efforts in both research and education.

Systematics is *the* science of biodiversity. To be sure, other biological, chemical, and physical disciplines provide supporting data. However, systematics (which is the study of phylogenetic relationships among species and among natural groupings of species, and the development of classifications based on those relationships) is most directly concerned with the legacy of biological diversification on earth. Systematics specifically informs decisions regarding the use and preservation of genetic diversity of cultivated plants, domesticated animals, wild progenitors of these species, and the closest relatives of these wild progenitors. In addition to such taxa of obvious value to humanity, intelligent decisions concerning the use or preservation of *any* species hinge on the existence of a fundamental understanding of species boundaries, species origins, and species relationships.

Pressures of development are causing an alarming increase in the

rate of species extinction. Loss of biological diversity is a disaster, both from the commonly cited economic standpoint (the potential extinction of many organisms useful for food, medicine, or technology) but also from a broader intellectual standpoint—all living things are *literally* our relatives, and one of our biggest and potentially most satisfying intellectual challenges is to know their (and thus our) genealogy. Fortunately given the timing of the current crisis, newly developed methods for data gathering and analysis of phylogenetic relationships (i.e., the genealogy of species) position us on the threshold of a deep understanding of the history of the biological world. Just in the nick of time, we are moving towards improved classifications of organisms and improved means of applying this knowledge to their conservation.

In this paper I will address each of the three subtitles to the symposium: research, education, and conservation, in both a general and a specific context (i.e., how can we at the Jepson Herbarium and the University of California address these concerns?). Each of these issues revolves around *the* fundamental task of systematics: *phylogeny reconstruction*. Since this connection is not widely realized by either the general public or botanical specialists, I need to begin by explaining the principles of modern Hennigian phylogenetics and then explore its role as a basis for setting conservation priorities.

PHYLOGENETIC SYSTEMATICS

The field of systematics underwent a conceptual upheaval in the 1970's and 1980's—for an insightful history, see the masterful book by David Hull (1988). Many issues were at stake in the “systematics wars,” foremost of which was the nature of taxa. Are they just convenient groupings of organisms with similar features, or are they lineages, marked by homologies? The consensus view these days among most systematists is that taxa are the latter, but why? Why is phylogenetic integrity necessary for species and other taxa? Taxa could, of course, be whatever we want, since the whole nomenclature system is a human construct (i.e., the naming system *is* a series of legislated conventions, even though the units being named may well be real). Many kinds of non-phylogenetic biological groupings have been proposed that are unquestionably useful for special purposes (e.g., “predators,” “rain forests,” “succulent plants,” “bacteria”). However, phylogenetic systematists (cladists, the great majority of systematists now) have settled on phylogeny as the best criterion for general purpose classification. Understanding why this choice was made requires some background.

Like other cutting-edge areas of biology, phylogenetic systematics is loaded with terminology and quantitative methods, yet the basic principle is quite simple (for further information see Wiley 1981;

Funk and Brooks 1990; Brooks and McLennan 1991; Mishler and De Luna 1991; Mishler 1994). The fundamental idea is known as the *Hennig Principle*, and is as elegant and fundamental in its way as was Darwin's principle of natural selection. It is indeed simple, yet profound in its implications. It is based on the idea of *homology*, one of the most important concepts in systematics, but also one of the most controversial. What does it mean to say that two organisms share the same characteristic? The modern concept is based on evidence for historical continuity of information (Van Valen 1982; Roth 1988); homology would then be defined as a feature shared by two organisms because of descent from a common ancestor that had the feature.

Hennig's seminal contribution (Hennig 1966) was to note that in a system evolving via descent with modification and splitting of lineages, characters that changed state along a particular lineage can serve to indicate the prior existence of that lineage, even after further splitting occurs. The "Hennig Principle" follows from this: homologous similarities among organisms come in two basic kinds, *synapomorphies* due to immediate shared ancestry (i.e., a common ancestor at a specific phylogenetic level), and *symplesiomorphies* due to more distant ancestry (Fig. 1). Only the former are useful for reconstructing the relative order of branching events in phylogeny—"special similarities" (synapomorphies) are the key to reconstructing truly natural relationships of organisms, rather than overall similarity (which is an incoherent mixture of synapomorphy, symplesiomorphy, and non-homology).

In the Hennigian system, individual hypotheses of putative homology are built up on a character-by-character basis, then a congruence test (using a *parsimony* principle) is applied to identify *homoplasies* (i.e., apparent homologies that are not congruent with the plurality of characters). One advantage of this approach is that it is applicable to all data types, ranging from traditional anatomical characters to alternative nucleotides at a homologous position in a DNA molecule (and phylogenies are best inferred from combinations of such diverse data types; Donoghue and Sanderson 1992; Mishler 1994). All that is required (in the phase of phylogenetic research commonly called "character analysis") is evidence for: (1) homology and heritability of a character across the taxa being studied, (2) independent evolution of different characters, and (3) presence in each character of a system of at least two discrete states.

Finally, classifications are applied to the resulting branching diagram (*cladogram*). A corollary of the Hennig Principle is that classification should reflect reconstructed branching order; only *monophyletic groups* should be formally named. A strictly monophyletic group is one that contains all and only descendants of a common ancestor; these are groups recognized by synapomorphies. A *para-*

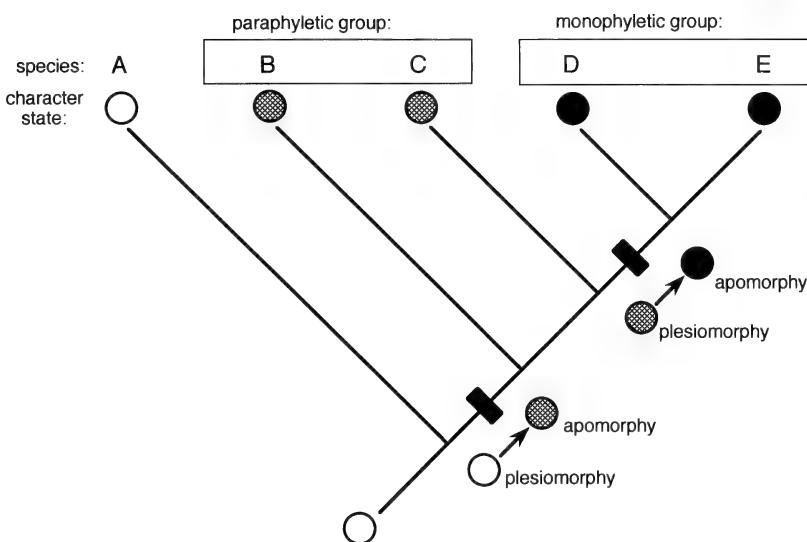


FIG. 1. A hypothetical cladogram illustrating definitions given in text. Shown is a phylogeny of five species (A–E) based on a number of characters. One character is mapped onto the cladogram; two evolutionary changes occurred in this character, giving it a three state transformation series (shown for generality as an open circle, partially-filled circle, and completely-filled circle—in reality this would be something like three different stamen numbers in the flower or three different nucleotides at one site in the DNA). These changes illustrate the relational nature of the distinction between plesiomorphy and apomorphy: initially, the partially-filled circle would represent the apomorphic state (relative to the open circle) at that branch of the phylogeny, but it would represent the plesiomorphic state at a later branch of the phylogeny (relative to the completely-filled circle). Two of the many possible higher-level groups are shown: a group D–E (supported by the synapomorphic final state in the transformation series) would be monophyletic, while a group B–C (supported by the symplesiomorphic intermediate state in the transformation series) would be paraphyletic.

phyletic group is one that excludes some of the descendants of the common ancestor; these are groups at best marked by symplesiomorphies. See Fig. 1 for the distinction between these two types of groups.

This elegant correspondence between synapomorphy, homology, and monophyly is the basis of the cladistic revolution in systematics. By restricting the use of the formal Linnaean system to hypothesized monophyletic groups, we can most efficiently summarize known data about attributes of organisms and also predict unknown attributes. For a recent example (from Systematics Agenda 2000, 1994), taxol (the drug used to control ovarian and breast cancer) was discovered in the bark of *Taxus brevifolia*, pacific yew. Three trees were needed for each patient, which was fatal for the trees at least, and could

have lead to endangerment of the species. A random search for a source for taxol in other trees in the same environment would have taken years, but a search based on an understanding of phylogenetic relationships lead quickly to the European yew (*Taxus baccata*), which turned out to be a better source because the leaves could be used (a renewable resource).

Phylogenetic taxa are "natural" in the sense of being the result of the evolutionary process. Evolution by natural selection might under some extreme conditions cause organisms to become very similar in some respects even though they are unrelated. But such similarity will not be across the board, but rather in the suite of attributes being influenced by convergent selection (e.g., a hummingbird pollination syndrome, thorns, or succulence). Across the board, detailed similarity is more likely to be due to descent (homology; synapomorphy) than common environment (analogy). This is true for either morphological or molecular data; contrary to common perceptions, our recent, rapid progress in understanding relationships in plants is due less to the new sources of molecular data than it is to the new cladistic methods of analyzing data.

Phylogenetic criteria are necessary for the designation of taxa at the species level as well, although the details of applying the concepts of monophyly and apomorphy at that level are controversial and beyond the scope of this paper (see Mishler and Donoghue 1982; Mishler and Brandon 1987). The gist of the matter is that species taxa, like higher taxa, should be distinguished by distinct, apomorphic character states rather than by overall similarity. Thus traditional botanical concepts that view species as either clusters of similar plants or as sharing a common breeding system need to be re-examined, since these types of similarities are often plesiomorphic.

PHYLOGENETICS AND CONSERVATION BIOLOGY

There is a widely perceived dichotomy between academic phylogenetic systematic studies and applied studies of floristics and plant conservation. This division has been aggravated by misunderstandings on both sides: academic researchers have been known to disdain concerns about utility of classifications, and resource managers have been known to complain about nomenclatorial changes resulting from improved taxonomic understanding. However, for efficient progress in the urgent business of plant conservation, it is important to recognize that practical issues such as identifying plants, making lists of species, and developing conservation plans *are* affected by the theoretical considerations discussed in the previous section. We don't want just *any* old name for these purposes, but rather a good name, one that reflects a natural phylogenetic entity. With natural

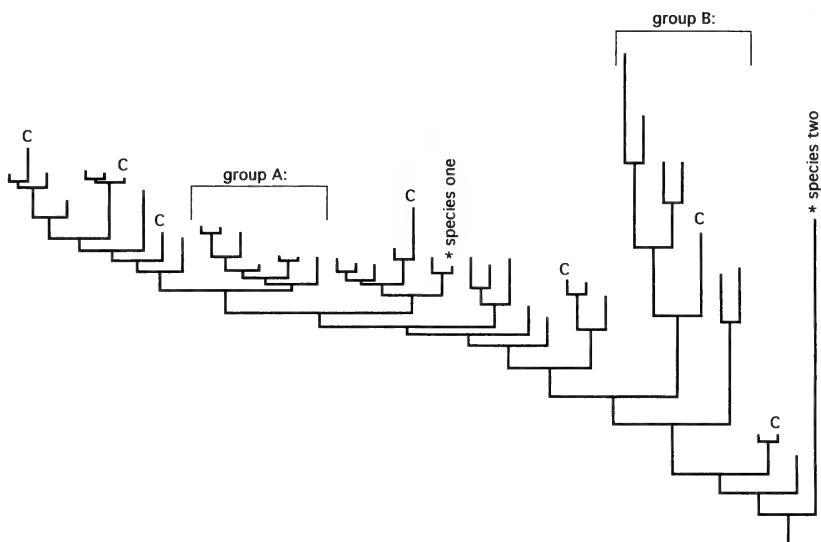


FIG. 2. A hypothetical cladogram illustrating the importance of phylogeny in setting conservation priorities. Shown is a phylogeny of 43 species; the branch lengths are proportional in the vertical direction to the number of evolutionary character changes along that branch. From the standpoint of preserving the maximum amount of phylogenetic diversity (and its closely associated genetic, morphological, physiological, and ecological diversity), species one would have a lower conservation priority than species two. Three groups of seven species each are also marked on the cladogram. By the same criterion, group A would have a lower conservation priority than group B. Group C, consisting of the same number of species scattered across the cladogram, would have a much higher conservation priority than either group A or B. In fact, group C would have a higher conservation priority than groups A and B *taken together*. Thus, the number of species in a locality is by itself a poor indicator of its priority for conservation (see text for further explanation).

taxa, one can rationally talk about issues such as evolution, biogeography, and extinction. With unnatural taxa (i.e., artificial assemblages of unrelated populations) such issues are meaningless, and conservation efforts are hampered at best (and misguided at worst). Without knowing the relationships of populations and species, there is no practical way to conserve them. We need to set priorities.

All species are not equal in a phylogenetic sense (or any other sense for that matter; e.g., Mishler and Donoghue 1982). As has been pointed out by a number of pioneering cladistic conservation biologists (Vane-Wright et al. 1991; Faith 1992a, 1992b), conservation priorities can best be set by a consideration of the phylogenetic relationships among species. This is because all attributes of organisms (genetic similarities, ecological roles, morphological specializations) tend strongly to be associated with phylogeny. As pointed

out by David Wake (personal communication), from the standpoint of preserving the maximum phylogenetic diversity (and its associated attributes), saving a long-branch species (i.e., one such as the coast redwood or Santa Lucia fir with much change along the terminal branch, either due to extinction or rapid evolution) should carry a higher priority than saving a short-branch species (i.e., a goldenrod differing in only a few minor features from near relatives). Furthermore, saving a community of 100 species of diverse phylogenetic relationships should carry a higher priority than saving a community of 200 species belonging to only a few large genera (see Fig. 2 for an illustration of these points). Thus, systematic considerations should play a much more important role in conservation biology than they have to date (e.g., there are whole books devoted to the field that do not even mention this key role of phylogenetic systematics).

In an ideal world all species could be preserved—in this world of limited resources (time, money, and public goodwill) an index based on phylogeny must be developed to help us preserve the maximal genetic, morphological, chemical, and ecological diversity. The general public will be much more supportive of species preservation efforts that are carefully focused and justified in this way, rather than of uncritical, across-the-board efforts. Phylogeny reconstruction is thus not just an academic exercise, but rather the fundamental basis of a truly practical taxonomy.

EDUCATIONAL NEEDS

A major international planning effort has been taking place over the last three years to define a clear set of attainable goals in systematics. This effort is entitled *Systematics Agenda 2000*, one major component of which will be in the area of enhancing research centers for systematics (with their associated collections and databases); another of which will be in the area of education (training an expanded work force in a broad array of necessary skills). There are a number of productive and influential systematic research centers in California, yet only a small handful of universities have retained strong, broad-based systematics programs and are thus poised to respond to the current educational challenges. California's biodiversity is currently at great risk, and those few centers of research excellence in systematics that are also associated with first-class education programs have an especially important role to play.

Because of its unusual combination of attributes, with large herbaria and botanical garden as well as a number of supporting laboratories located within a major research university, UC Berkeley can make a unique contribution within California (and indeed the western United States) to these educational challenges. What, in

particular, can the Jepson Herbarium contribute? One obvious area is in research, but since this area has always been a focus and is being addressed by other papers in this issue, I will emphasize another area that has not been a historical focus of the Jepson Herbarium: education.

General educational needs can be placed into six categories, as follows:

1. *Ph.D. studies.* The need to train specialists in systematics to "read" the biological information present in natural diversity has never been greater. Systematists must have a range of technical skills to extract information at all levels of inquiry (e.g., DNA sequences, organic chemistry, anatomy, morphology, ecology) and a broad theoretical background to interpret this information correctly. Modern biological systematics integrates a diverse array of disciplines ranging from molecular, cell, and developmental biology, to ecology, evolutionary biology, and philosophy. Data-gathering techniques are becoming increasingly diversified, complex, and numerical (even though field studies of ecology and distribution remain as important as ever). Specialists need to be trained in all groups of organisms, plants as well as the more popular animal groups, cryptogams as well as the more heavily studied flowering plant groups.

If graduate students are to integrate subjects, they have to be proficient in them. Accordingly, students of evolutionary processes and products all should obtain backgrounds in population biology, biogeography, paleontology, phylogenetics, and systematics. The identification of critical phylogenetic problems to apply new techniques to, and the integration of new data into an existing morphological framework, are only possible through such in-depth training in both the conceptual basis of systematics and the biology of some specific group of organisms. Attaining such breadth and depth requires a research university with a spectrum of faculty specialties; such a spectrum is represented in the biology departments at UC Berkeley, particularly in Integrative Biology and Plant Biology.

With the addition of several new faculty (myself, Bruce Baldwin, and a new systematic mycologist in the University and Jepson Herbaria; Nan Arens in the University Museum of Paleontology) to the existing faculty in plant systematics and evolution, we can provide an outstanding graduate program in this traditional emphasis of a research university. However, we must not forget other areas where we can make a contribution.

2. *Postdoctoral studies.* An important part of a complete education in a synthetic discipline such as systematics is a postdoctoral period of training. This appears to be the ideal time for a generally trained systematist to become familiar with a new technology to apply in their specialty. There is a two-way relationship between postdocs and an institution. The postdoc is benefited by working in a different

intellectual environment, learning new techniques, and having a relatively unfettered period of time to complete and publish research before taking a professorial position. The institution benefits from having new Ph.D.s bring fresh ideas and expertise into its program, which is stimulating for both faculty and graduate students. We need to find the resources to make this a viable part of our program in plant systematics.

3. *General training in systematics for other biologists.* The recognition is dawning that an understanding of systematics is just as important as statistics or chemistry in the required background knowledge for all biologists, even those who will specialize in other areas such as medicine or biotechnology. Any biological study that compares two or more organisms, or even studies on a single organism that will eventually be consulted by biologists interested in other organisms, should incorporate some elements of systematics. Examples include the use of the systematic literature to intelligently select study systems, positive identification of study organisms by specialists (with application of correct nomenclature and deposition of voucher specimens in a permanent collection), and the use of appropriate concepts of taxa (especially at the species level) and formal comparative methods to determine the generality of study phenomena (e.g., Brooks and McLennan 1991). A phylogenetic tree produced from an analysis of the relationships of species constitutes a pattern of descent (common ancestry), modification (changes in ancestral characters), and spatial relationships (patterns of biogeography). In theory, all changes (anagenetic as well as cladogenetic) that occur during evolutionary descent can be incorporated into this tree. This allows investigators to assess the extent to which either recent or historical factors have influenced the relationships among groups or between the ecology and phylogeny of a single group. We intend to continue inserting such principles of systematics into the large Integrative Biology undergraduate major at UC Berkeley, as is being done in an increasing number of institutions across the state.

4. *Professional training in areas such as curation, environmental assessment, and conservation biology.* There is a growing need for professionals in these areas, requiring very different training than that necessary for the Ph.D. route. In fact, the specialization required these days for the latter route is such that Ph.D.'s are usually not well-equipped to carry out broad inventories. This distinction is not meant to denigrate either route, or to downplay the obvious connections between them detailed earlier; it is merely a recognition that the field is too big to comprehend all at once and that a division of labor is called for. The training needed to carry out a high-powered monographic and phylogenetic study of one group of plants is just different than the training needed to carry out a cutting-edge environmental inventory and conservation plan for many groups of plants.

Several campuses of the California State University system have traditionally had strong Master's programs in these areas, while UC Berkeley has not. We hope to rectify this gap here; I am looking into the feasibility of beginning a collaborative program in these areas, probably in connection with the UC Botanic Garden and the UC Extension program. The general idea would be to have students take a program of courses in systematics, ecology, and some environmental policy, with an intervening summer used for practical experience (e.g., an internship to learn about curation, environmental impact statements, field work, or specimen-based research). Such a program has the potential of being a model for the future; it should offer unique opportunities and thus be popular enough to be self-supporting. We are asking for feedback and assistance in setting this up in a maximally useful way.

5. *Educational programs for interested amateurs.* There is a great deal that can be (and has been) contributed by trained amateurs, in areas such as documenting precise geographic ranges of species, discovering new variants, and testing new uses for wild species in horticulture. To this end, we will use the resources of the Jepson Herbarium to offer courses in systematics. For example, the Weekend Workshops on systematics of specific problem groups, designed for both the professional botanist and the interested amateur, are our first attempts in this area. We hope this series will be the first of many general courses of this nature, and again would be glad to have feedback on how we could best serve your needs.

6. *Educational programs for school children.* Many youngsters (especially in the minority community from inner city schools) never have the chance to consider professional opportunities in organismal botany, because they get no exposure to these areas in school or at home. An understanding of the scientific study and importance of biodiversity should be an important part of the curriculum for all students. We plan to reach out to the local high schools first, partly because there are fewer of them than elementary schools, but also because this is a key age for career choice. Reaching out to the elementary schools would require the development of a docent program, and it may be that we can join forces with the already excellent programs for elementary school children put on by the UC Botanical Garden.

We, the staff, associates, and friends of the Jepson Herbarium, need to take advantage of the currently expanding concerns for the study and preservation of biodiversity among the public, and take a leadership role in the state of California and the United States in general. In doing so we must channel the public's rather unfocused concerns through educational efforts at all these levels. There is only a limited amount of time within which to save the diversity of native plants that remains in California. We need to concentrate on those

areas in which a university-associated herbarium can make a unique contribution. We will continue the tradition of rigorous scientific *research*, augmented with new concepts and technologies. Furthermore, we will pursue innovative ways of organizing and presenting information about California plants. We will develop enhanced *education* programs, as detailed previously. And finally, we will relate and focus these research and education efforts on one of the most critical problems facing California today: the *conservation* of its diverse, beautiful, and useful flora.

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(Received 7 Oct 1994; accepted 3 Feb 1995)

THE CHANGING FACE OF CALIFORNIA BOTANY

BARBARA ERTTER

University and Jepson Herbaria, University of California,
Berkeley, CA 94720-2465

ABSTRACT

Botany in California has already gone through several faces, and is changing still. The first face was the folk knowledge held by the original inhabitants, largely obliterated during subsequent periods. The first century of European exploration resulted in specimens being deposited in European herbaria, clearinghouses for Linnaeus and subsequent experts. This shifted in the mid-nineteenth century, when the United States annexed the western half of the continent. Specimens collected as part of army-assisted territorial and state surveys now flowed to Torrey and Gray in the eastern United States. By the turn of the century, however, resident botanists in California began to resist Eastern hegemony and to establish their own networks of collaborators. The continued inclusion of numerous amateurs in these networks helped to counter the growing tide of professionalization that was otherwise changing the Face of Academic Botany. Instead, "professional" and "academic" are no longer synonymous, such that there are now more botanists employed by government agencies than by academic institutions in California, primarily because of the increased interest in endangered species. The latest face of California Botany is therefore that of a developing partnership between academic botanists, non-academic professionals, and native plant enthusiasts.

The topic of this paper, "The Changing Face of California Botany", is two-fold. On one hand, "The Changing Face" refers to various stages in the historical development of botany in California. This in turn leads to the second aspect, a summary of the currently developing "New Face of California Botany", which is itself a result of the interplay of two threads. One thread is the historical development of botany as a formalized, professional science, the province of academia. The other thread is the concept of botany as the cultural knowledge of plants that is the province of the general population.

In this latter sense, the first experts on the California flora were the Ohlone, Miwok, Wintu, and other manifold tribes that originally occupied the region now called California. Each tribe knew the flora of its territory intimately, as the source of food, fibers, medicine, and many other essentials of life (Blackburn and Anderson 1993). As in the rest of the world, the first Face of Botany was therefore not a specialized branch of learning belonging only to an elite intelligentsia. Taxonomic and floristic information was part of the essential cultural heritage of a society, amassed and transmitted orally over the span of uncounted generations.

As an ironic result, the Great Period of Exploration of the Cali-

fornia Botany by western Science was actually a period of net *loss* of knowledge of the California flora, as the indigenous cultures were decimated and their knowledge was destroyed. This point was brought home to me when a reporter asked if the Indians had any uses for the Shasta snow-wreath, and I realized that, even though the species had just been "discovered", the local tribes undoubtedly had been familiar with the shrub and very probably had some use for it about which we will never know.

Western science began the long process of learning the California flora from the seeds and pressed plants sent back in the 1700's and 1800's by European exploring expeditions, seeking profitable trade items and lands to claim. During this period even the coast of California was a long, long way from centers of Western civilization. The Panama Canal did not exist, so the entire coast of South America was more accessible than was western North America. It wasn't until Spanish missions and British trading posts had been established along the Pacific Coast of North America that more extensive botanical expeditions were possible, by such well-known collectors as David Douglas from Scotland, and Thomas Nuttall, an Englishman working out of Philadelphia and Harvard (McKelvey 1955).

Nuttall was anomalous in that he both collected and described his own material. This was contrary to the dominant pattern initiated by Linnaeus, who depended on the steady stream of novelties collected by his disciples and correspondents from around the globe. This system of an institution-based expert providing a clearinghouse for a network of field-based contributors proved to be very effective, and occurs as a repeatedly appearing pattern. The logic here is that plant exploration requires covering vast areas, generally far from population centers, but the analysis of the resultant collections requires the resources of a major herbarium, with abundant comparative material and library facilities. The initial cataloguing of the New World flora therefore occurred as a function of on-site collectors sending specimens to the great herbaria in Europe, and this is why the types of so many Californian plants are to be found in Great Britain, Switzerland, France, Germany, Spain, Russia, and the Czech Republic.

The first United States expedition to California didn't occur until 1841, as part of a sea-based exploration under the command of Charles Wilkes. The abundant biological and anthropological specimens collected by the Wilkes expedition throughout the Pacific Basin are what triggered the establishment of the Smithsonian Institution. One of the plant novelties discovered in California was *Darlingtonia*, the cobra lily.

On the heels of the Wilkes expedition were three U.S.-sponsored overland expeditions led by John Charles Fremont, who had been trained by John Torrey in plant collecting techniques. Fremont, one

of the more colorful personalities in the history of the western United States, is better known as an instrumental figure in the seizure of California from Mexico, eventually becoming a senator and presidential candidate.

This marks the beginning of a major transition, intertwined with the United States' vision of Manifest Destiny. In fact, the driving force behind the aforementioned expeditions was less a spirit of scientific inquiry than a necessary precursor for expansionism. The discovery of gold in California (including some on Fremont's property) made an already swelling tide of immigration from the existing United States unstoppable. By the time the dust settled, the United States spanned the continent, including territory formerly claimed by Great Britain, Mexico, Spain, France, and even Russia (not to mention the uncounted Native Americans).

The impact of American expansionism on California botany took several forms. First was an increase in government-sponsored surveys. From our current perspective, it is somewhat a surprise to realize that many of these were army projects. In addition to surveys of newly established borders, the need to keep the expanded nation united spurred a series of expeditions to survey potential railroad routes. Thanks in large part to pressure on Washington exerted by Torrey and Gray, most surveys incorporated a botanical component, or at least allowed a botanist to accompany them and thereby take advantage of the military protection provided (McKelvey 1955).

The sporadic collecting in disputed or unclaimed territory before 1850 therefore gave way to a new face, that of major government-funded expeditions surveying newly annexed lands. This included state as well as federal activities; the new state of California, for example, established a State Geological Survey in the 1860's (Farquhar 1966). The underlying justification was to discover where the gold was, but a major botanical survey was accomplished at the same time by William Brewer and his successor Henry Bolander. One result was the first flora written for a western state (Brewer et al. 1876, Watson 1880).

Another aspect of the new face was that specimens collected on both national and state surveys during this period flowed no longer to Europe, but to respected botanists at established herbaria in the eastern United States. Asa Gray's influence grew as his mentor Torrey's waned, and for nearly 30 years Gray's hegemony dominated American botany (Dupree 1959). This, however, was already changing to yet another New Face by the time of Gray's retirement in 1873.

The most significant break from Gray's former hegemony came from the West itself, where the population had (again) grown to the point of supporting resident botanists. Although the great eastern botanical institutions at Harvard, New York, Washington, and Mis-

souri jostled to divvy up North America among themselves, paralleling European colonialism of previous centuries, autonomous centers had already begun to develop in California. As early as 1853, the California Academy of Sciences was established by a group of resident scientists, including botanist Albert Kellogg. Although some of his novelties were sent to Torrey and Gray for publication, Kellogg described several new species himself.

Kellogg was overshadowed in this regard by Edward Lee Greene, the first professor of botany at the University of California following its establishment in 1868 (Constance 1978). Greene, at the forefront of dissidents against Gray's hegemony and Eastern domination of Western botany, fought vitriolicly, not only with Gray but with other Californian botanists, such as Katharine and Townshend Brandegee.

When Greene took a position on the East Coast (unfortunately taking his herbarium with him, now at Notre Dame), he was succeeded by his first student, Willis Linn Jepson, who continued as Professor of Botany for over 40 years. Jepson himself represented a new face of western botany, in that he was a native Californian, with a native's love of the region extending well beyond mere professional interest. Jepson claimed hegemony over California, established Berkeley as a clearinghouse, and developed his own network of contributors and collaborators.

Overlapping Jepson's period of activity, primarily floristic in nature, was a major new development, the evolution of the current face of academic botany. This was "the New Botany", championed by Charles Bessey, with the goal of creating a true science of botany, characterized by explicitly objective and experimental methodologies comparable to those being developed in other scientific disciplines. Within academia, the field blossomed; where "botany" had once been synonymous with plant collection and classification, it now expanded to include what would become the subdisciplines of plant anatomy, physiology, genetics, and ecology.

Plant taxonomy became plant systematics, marked by the repeated introduction of new techniques offering increased precision, rigor, and objectivity. The first major step in this direction was actually pioneered in California, where the seminal experiments in biosystematics were carried out by Jens Clausen, David Keck, and William Hiesey (1940). Cytogenetics followed, and then chemotaxonomy. Computers triggered the development of phenetics and cladistics, both pre-adapted to handle the wealth of point-data now being generated by a diversity of molecular techniques.

The professionalization of botany within academia has been an essential step in establishing botany as a legitimate science, and the New Systematics has generated answers to questions that had previously proved intractable. However, the priorities of the New Systematics put a limit on how much time a modern systematist in

academia can devote to such time-consuming activities fundamental to basic taxonomy as general botanical exploration, specimen collecting and identification, preparing monographs and floras, learning the local flora, and annotating herbarium specimens.

On the other hand, plant taxonomy in the strict sense has never existed as an exclusively academic pursuit. Even Linnaeus depended on an extensive network of field-based contributors, a pattern that appeared repeatedly. In fact, the perception of botany as a professional academic activity is a relatively recent phenomenon, a corollary of New Botany. This is the subject of Elizabeth Keeney's (1992) book, *The Botanizers*, as described in these quotes:

In the years following the Civil War, two changes occurred that would have a dramatic impact on amateur botanizers: the historic patterns of information flow that had kept amateurs within the botanical community eroded, and the type of science pursued by amateurs was no longer that pursued by the mainstream of professionals . . . This development was by no means confined to botany, but rather was part of the normal process of professionalization, occurring across the disciplines; increasingly, those who saw themselves as professionals sought to set themselves apart and to establish their social position by preempting information and by claiming expertise. [p. 123]

The New Botany became the body of knowledge and techniques in which only professional botanists were expert, giving them the authority and autonomy that distinguished them both from amateurs and from other professionals in the life sciences. Only professional botanists were members of the 'ongoing community of inquiry' delineated by the New Botany. It defined the discipline in a way that promoted professionalization and discouraged amateur participation. [p. 149]

Although the schism between professional and amateur as described in *The Botanizers* is relatively accurate for plant sciences in general, in taxonomy the situation is neither as well-defined nor particularly straight-forward, especially in the western United States. Botanizing has continued to flourish outside of academia, in the form of numerous Native Plant Societies and conservation organizations, such that the membership of the California Native Plant Society far exceeds that of the California Botanical Society. Even within academia, the dichotomy between professional and botanizer is not clear-cut, in that much of the basic taxonomy still being done under the aegis of academia has personal satisfaction rather than professional advancement as a reward.

In California, non-academic botanizers have therefore never been completely isolated from professional taxonomists. Jepson, for ex-

ample, cultivated botanizers as part of his network, as did subsequent curators. Alice Eastwood at the California Academy of Sciences likewise encouraged the involvement of amateurs, and her protege John Thomas Howell continued to provide an outlet for the taxonomic contributions of amateurs.

Even more significant, however, is the fact that "professional" and "academic" are not synonymous. In fact, this currently developing new face of California botany represents a change as fundamental as that triggered by Bessey's *New Botany*, that of a collaborative partnership between academia, non-academic professionals, and talented amateurs.

As evidence for this statement, there are now more botanists in California working for various federal and state government agencies than there are in academic positions. The U.S. Forest Service alone employed 24 full-time and 60 seasonal botanists in California as of 1993 (J. Shevock, personal communication); add to this the increasing number of botanists working for the U.S. Fish and Wildlife Service, the Bureau of Land Management, and the California Department of Fish and Game (which includes the Natural Diversity Database). Nor should one overlook the increasing number of talented botanists employed by the private sector, primarily environmental consulting firms.

This changing face is both a cause and a result of an awareness of environmental issues, primary involving endangered species. Suddenly everyone is obligated to pay attention to rare taxa, with the result that basic plant taxonomy is now RELEVANT. Gone are the days when a taxonomist could make species calls right and left in blissful isolation, ignored by anyone but another taxonomist. Nowadays you might find yourself having to defend the validity of your new species in a lawsuit, or at least in front of the California Fish and Game Commission.

The resultant interplay between academic and non-academic botanists manifests itself in several ways in California. Academia continues to be the primary source of expertise and training needed by non-academic botanists, and the herbarium itself is an important source of fundamental taxonomic information that serves as a bridge between academic and non-academic interests. At the same time, as it did in the days of Linnaeus, Torrey, and Gray, academia still depends on the efforts of outside collaborators, who are simultaneously the main consumers of taxonomic products such as new species descriptions, keys, and floras. This includes computerized incarnations that comprise yet another New Face of California Botany.

As a primary example of collaboration, consider one of the most recent floristic efforts, the revised Jepson Manual (Hickman 1993), of which the first printing of 7,000 copies sold out in only 3 months.

For background, the terms of Jepson's endowment to the University of California stipulated that the original Jepson Manual (Jepson 1925) be updated and that his multi-volume Flora of California be completed. However, the activities necessary to meet these terms were not compatible with professional advancement, so neither Manual nor Flora were priority items for subsequent endowment-funded curators.

To become a reality, the Jepson Manual Project depended largely on grass-roots funding from non-academic sources within California, with mainstream NSF funding only at the tail end. And the funding provided only for the infrastructure, the editing and coordinating of treatments provided by nearly 200 unpaid contributors who provided the bulk of the actual text. As a rough calculation, only about half of these contributors were faculty or research staff at academic institutions, and this is including emeriti, non-systematists, and faculty at colleges too small to have an adequate herbarium. The remainder consisted of non-academic staff, consultants, agency botanists, students, and miscellaneous contributors, all of whom prepared treatments on their own time (as, for that matter, did many of the faculty and research staff).

As a second example of collaboration, consider the most fundamental contribution to conservation that taxonomists make: the initial recognition of previously unknown taxa. At present, new plant species in California are perhaps more likely to be discovered and described by agency botanists, environmental consultants, horticulturalists, and native plant enthusiasts than by academic botanists. For example, academia cannot take credit for the recent headline-making discovery of the Shasta snow-wreath, *Neviusia cliftonii* (Shevock et al. 1993), but at the time there were no academic systematists specializing on the California flora at any of the major herbaria in California. The discovery itself was by two consultants, while the senior author was a forest service botanist.

The snow-wreath collaboration continued through the following year, with an announcement that anyone wanting to assist in the search for new populations should congregate at a group campground that had been reserved by the local forest service botanist (Shevock 1993). The forest service also provided a boat to ferry participants across Shasta Lake. Nearly 50 botanists showed up, mostly agency botanists and consultants on busman's holiday. As a result, five new populations were discovered, bringing the total known to eight.

This kind of distributional data is one more example of taxonomic information that is relevant to conservation, as a key to determining what plants are rare enough to deserve special consideration. In California, the primary published summary of rare plants is the California Native Plant Society's "Inventory of Rare and Endangered Vascular Plants of California" (Skinner and Pavlik 1994). In

addition to the personal expertise of numerous collaborators, both academic and non-academic, one of the greatest sources of information for this on-going effort has been the collective holdings of California herbaria. However, the millions of specimens comprising the collective holdings of herbaria worldwide, overwhelming as they are, nevertheless are only an erratic sampling of actual distributions. Often they are more an indication of who collected where than what grows where, as proven by how long *Neviusia cliftonii* remained undiscovered.

Distributions compiled from existing herbarium specimens are sometimes inadequate in another way, as illustrated by *Horkelia cuneata* Lindley ssp. *puberula* (Greene) Keck. It is not currently on any rare plant list, largely because there are plenty of herbarium specimens of the taxon. However, most of these specimens are from the Los Angeles Basin, which should quickly alert anyone familiar with the area that the current distribution may be decidedly otherwise. Nobody has checked to see how many historical records still represent extant populations; I suspect that the subspecies may be in serious danger.

A final example of the political, economic, and legal ramifications of taxonomic decisions, and the way that taxonomists are being called into the fray, is the case of *Chorizanthe robusta* C. Parry var. *hartwegii* (Benth.) Rev. and R. Morgan. When the California Native Plant Society petitioned the U.S. Fish and Wildlife Service to have the variety emergency-listed, the consulting botanist who had encountered some on a proposed development site countered that the variety was actually a trivial variant in a species that had been too finely split.

The Fish and Wildlife Service did not have the expertise to break the impasse on their own. What they did instead was arrange to have three taxonomists (Lincoln Constance, Larry Heckard, and myself) spend a day examining all relevant material. Our conclusion was that the variety was indeed so weakly delimited as to sit right on the cusp of being worth naming or not. We bypassed the problem, however, by noting that most of the known populations of *C. robusta* as a whole had been extirpated, as had those of the closely related *C. pungens* Benth. We therefore recommended that the entire complex be petitioned for listing. This is, in fact, the course that was taken, and as a result all varieties of both species have recently been Federally Listed.

In summary, the latest face in the ever-changing face of California botany is that of a developing partnership between academic botanists, non-academic professionals, and native plant enthusiasts. I deeply believe that such regional, collaborative efforts are integral parts of any realistic solution to the numerous environmental problems that are besetting us. In this regard, I can think of no more

appropriate ending for this symposium paper than to quote Jepson himself at the founding of the California Botanical Society (Anon. 1916):

A botanical society, said Dr. Jepson, ought to have two aims—the promotion of botanical research, and the diffusion of accurate botanical knowledge, in an accessible form, amongst the people. Botany should not be the property of a small cult or a select few, but it should be a science with a broad outlook in its relation to other sciences and to the humanities. It should play its due part in the progress of civilizations in California.

With any such end in view botanical science, for its proper development, must have the support of the people of California, with such support accorded, the people of California are entitled to have at their command the best results of recent botany in a form suited to their needs.

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(Received 1 Aug 1994; accepted 3 Feb 1995)

COLLABORATION AMONG HERBARIA AND BOTANICAL GARDENS

GEORGE K. ROGERS

University of California, Botanical Garden, 200 Centennial Drive,
Berkeley, CA 94720

ABSTRACT

As obvious as the desirability of collaboration among botanical gardens and herbaria may be, such collaboration is observed generally not to reach optimal levels. The scientific and research goals of herbaria as opposed to the public or broad-service orientation of gardens should not preclude active collaboration. Each needs the other for mutual advocacy. The data management challenges of the two are closely related, and we have reached a point where in effect all well curated natural history collections can be linked electronically into one large pool for sampling and data-retrieval purposes. This comes at a time when the value of living collections is on the rise for chemical and pharmacological research. Education is basic to all botanical activity, and joint programming is richer and is more efficient than the opposite, especially at a time when natural history education is interpretable as increasing in value to human society. If the need for humanity to relate more closely and respectfully to nature drives botany into increasing prominence, the impetus should not impact herbaria and botanical gardens independently, but rather as integrated representatives of botany, plant diversity, biodiversity, and nature.

The general desirability of collaboration among botanical gardens and herbaria is obvious. After all, herbaria and botanical gardens are among the few institutions dedicated to plant diversity. We have similar data management challenges: keeping track of the taxonomy, nomenclature, literature, origins, and whereabouts of vast numbers of plant specimens. Botanical gardens and herbaria are both prone to teaching about plants. We have common problems, including the joint need to promote botany in a highly competitive scientific world. We both are in positions to understand the diminishment of plant diversity, contemplate the consequences, and participate in plant-related conservation initiatives.

Why then is there not more collaboration among gardens and herbaria, even between obvious pairs? Perhaps the chief impediment is a fundamental difference in basic goals.

Even though botanical gardens and herbaria both deal with plant diversity, they differ in outlook and goals. Modern herbaria are scientific research institutions, with a primarily scientific audience, and tend toward increasing integration with other sciences. Their goals are comparatively clear. By contrast, many botanical gardens (or the cultivated components of herbarium/garden combos) have

undergone evolution and often diversification of purpose. Many started out as private horticultural estates, or as plant collections accumulated for relatively narrow purposes depending on a narrow, often private, funding base. Most botanical gardens now are publicly owned or subsidized, and must serve accordingly. Under the broad category of public service or service to the larger organizations to which they belong (such as city, county, or state governments, or universities), botanical gardens have diffuse goals, often mixed within the individual garden. The goals often have to do with ornamental horticulture or public interpretation. University gardens have the duties of facilitating teaching and research. Herbaria are project-oriented, and botanical gardens are service-oriented.

Pursuing our differing goals along different tracks is no reason to fail to strive to collaborate. On the positive side, our differences serve to minimize competition while leaving the door open to selective collaboration.

At the grossest level, a goal common to herbaria and gardens is financial well-being. If botany is seen as one small voice in a very big, highly competitive world of funding for science and education, the botanical voice should be harmonized. We need each other to promote the overall well-being of botany.

But more specifically, how can we help boost each other's goals? What can a garden offer an herbarium? Perhaps now more than ever living collections can be extensions of preserved collections and of each other, and thus broaden the pool of research resources. At the same time, research activities that make use of living plants appear to be on the rise: molecular work and plant-based pharmacology, are prominent examples. At present the University of California Botanical Garden receives about 70 requests per year for fresh research materials. As the data base improves, as our ability to share data improves, and as visibility of the collection improves, we expect demand to rise substantially. Overnight delivery services help compliance with requests. In a low-tech sense, herbarium researchers with convenient electronic and overnight-delivery access to living collections can always benefit by access to fresh, living plants as subjects for illustrations and photographs; as subjects for dissections, chromosomal, anatomical, or morphological work; as opportunities to settle questions or observe biological phenomena not answered by pressed specimens; as subjects for obtaining enhanced familiarity with taxa of interest; as a botanically inspiring setting for functions and visits; and for teaching.

An additional way that botanical gardens support herbaria is by serving as a public face for botany. Visits to botanical gardens are the only exposure to botany experienced by immense numbers of people. Most botanical gardens have public outreach programs, and most of the programs reach thousands of schoolchildren. At the UC

Botanical Garden, the figure is about 4,000 per year on school tours, apart from those coming for day camp, non-school activities, special programs, and with families. Drop-in visitorship is considerable. According to the International Directory of Botanical Gardens, the larger gardens in the U.S. each bring in well over 500,000 visitors per year. Most cities have one or more botanical gardens, and in the Bay Area, there are at least eight public gardens presenting botany and related subjects to hundreds of thousands of visitors. Beyond visitors, botanical gardens often issue public publications, and draw media attention. Media attention to the Missouri Botanical Garden alone has undoubtedly lifted the status of U.S. botany.

How then do herbaria contribute to the goals of a botanical garden? The need is embodied in the term "botanical garden." Botanical gardens often tend to drift from rigorous scientific botany. Few have the benefit of any or many plant taxonomists devoted to curation and programming. Gardens benefit enormously from access to practicing botanical scientists. Maintaining a living plant collection requires constant attention to plant identifications, taxonomic updates, and nomenclatural correction. At the University of California Botanical Garden, help from the UC herbaria has helped maintain curatorial quality, with ferns being the most recent example. And beyond curation, interpretation and education are far richer when herbarium-enriched.

Both types of institutions tend to be active educationally, and this happy business is a perfect opportunity to watch for collaborative possibilities. Gardens offer the perfect sites for botanical education, access to living plants, existing audiences, publicity devices, and expertise, including horticultural know-how, and experience with public programming. Herbaria can always provide a scientific perspective, and often well-traveled teachers with tremendous knowledge. Several herbarium researchers come to mind who are known to public audiences. Drawing upon both gardens and herbaria, it is possible to combine information on taxonomy with fresh, colorful living specimens, and it is possible to bring the broadest possible expertise to bear on subjects of common interest, such as local environmental issues, or popular plant assemblages such as orchids or California natives. A joint herbarium-garden program on a given plant group can span the spectrum from fine points of nomenclature, to ecology, to horticulture. Public consumers of plant-related programming don't see and don't much care about a distinction between botanical garden and herbarium. They are more interested in overall quality, in learning about plants, and in exposure to the people who know the most. Pooling educational resources works, because it costs little, and the payoff is undisputable.

To summarize, the time is right for herbaria and botanical gardens to find renewed interest in collaboration. Botany is not a high-budget,

high-profile science; we need a unified voice to be heard. And perhaps botany's star is on the rise as knowledge of plants becomes increasingly critical to grappling with problems of the 21st century: feeding and medicating 10 billion people, finding alternative fuels, and creating a green, healthy, and pleasing climate for humans and the rest of nature. The increasingly visible and increasingly promising human-oriented aspect of botany gives botanical gardens and herbaria new, intertwined opportunities. The potential roles of herbaria and gardens in all of that are tightly linked, since the grandest goals of botany must involve the broadest research resources possible.

(Received 19 Aug 1994; accepted 8 Feb 1995)

RARITY IN THE CALIFORNIA FLORA: NEW THOUGHTS ON OLD IDEAS

PEGGY L. FIEDLER

Department of Biology,

San Francisco State University, San Francisco, CA 94132

ABSTRACT

Rarity in vascular plant species can be caused for a variety of reasons, such as old age or habitat specialization, and many of these causes have been discussed for over a century. Some of the more insightful ideas about the nature of rarity have sprung from California botanists intimate with the California flora. New thoughts that have expanded on older ideas about rarity suggest that, as a biological phenomenon in the California flora, it is a polythetic expression of several limiting factors, including, but not limited to age of origin, habitat specificity, and possibly a limited genetic diversity. While efforts to catalogue rare plants in California is increasing our understanding of their biology as well as their threats, little attention is paid to unprotected, but possibly unique populations of common as well as rare species. Such populations may represent the beginnings of the evolution of new rare plant forms. Less vigilance in the protection of these populations may result in a decelerating rate of evolution of new rare plant taxa in California.

Rarity is really a statement about geographic distribution and abundance (Drury 1974, 1980; Fiedler 1986; Fiedler and Ahouse 1992). As such, it represents at least three different phenomena. Rare species may be restricted in distribution, but abundant where found, as illustrated by the *Calochortus tiburonensis*. Other rare taxa may be more widespread, but never abundant where found. Sparsely distributed taxa, such as members of the genus *Nolina*, including the rare *N. interrata*, are excellent examples. Finally, rare taxa are often very localized and represented by only a few individuals. These rarities are rather few in number, e.g., *Lilium pardalinum* ssp. *pitkinense*, and typically are considered the most vulnerable to extinction due to habitat destruction.

California hosts an exceptionally large percentage of rare taxa, and much has been written about California's unique and famously rich flora (e.g., Raven and Axelrod 1978; Stebbins 1978a, b). It is generally accepted, for example, that the most famous of California's rarities are either old species—i.e., paleoendemics (e.g., *Sequoia sempervirens*, *Sequoiadendron gigantea*), or new species—neoendemics (e.g., *Linanthus killipii*, various members of the genus *Lasthenia*, and many other taxa). The California flora serves as an excellent backdrop to review the older ideas concerning the phenomenon of rarity, as the various causes of rarity can be illustrated clearly. I use

the term "old" broadly, in part because this review spans only a century's worth of research and synthesis, and in part because the newer ideas about the causes and consequences of rarity fall immediately on the heels of the older ones. My designation of old vs. new may seem arbitrary, but it suggests that we are now moving in new directions in the understanding, and ultimately, the preservation of California's rare plants.

HISTORICAL REVIEW: OLD IDEAS

I have divided the historical ideas about rarity into five broad categories. The categorizations are not necessarily complete, but are meant to represent the major ideas concerning rarity in vascular plants.

Age. Charles Lyell (1830–1833) and Charles Darwin (1872) believed that being rare was the precursor to becoming extinct. In short, they suggested that species that had persisted for a long, but unspecified length of time, were by definition rare, and thus were soon to become extinct. The American botanist Merritt Lyndon Fernald, most famous for his revision of *Gray's Manual of Botany*, later agreed with Darwin and Lyell (Fernald 1950). In a long series of papers on the flora of the eastern United States, Fernald developed a theory of relictual endemism citing age and consequently poor competitive ability as the reason for rarity in vascular plants (e.g., Fernald 1918, 1925, 1942).

Conversely, other botanists argued that rare taxa can be newly evolved. As early as 1836, in his publication *New Flora of North America*, Constantine Rafinesque suggested that old species were those with the most numerous individuals, and therefore new species must be those with the fewest individuals, and therefore rare. The correlation between geographic distribution and taxon age was fully articulated by J. C. Willis (1922) in his "Age and Area" hypothesis. Thus the discussion concerning whether rarities were old or new (but not both) was rather hotly debated for several decades in the early twentieth century (see e.g., Gleason 1924).

Ecology. In the mid-1800's, the British botanist H. C. Watson examined the phytogeography of rare plants in the British Isles and determined that the rare plants on this island group were habitat specialists. This autecological concept was echoed and further embellished by Herbert Mason for California's rare plants. In this regard, Mason published a pair of articles in *Madroño* (1946a, b) in which he pointed out that much of California's floristic diversity was the result of the superimposition of both diverse and unusual lithic features upon a wide range of climatic conditions.

Another major ecological theory concerning the cause of rarity

has to do with the competitive ability of plants. This was first fully articulated by Robert Griggs (1940), but demonstrated by Arthur Kruckeberg (1951) experimentally for certain taxa restricted to ultramafic substrates (e.g., *Streptanthus polygaloides*, *Achillea millefolium*) in his now classic competition experiments.

Genetics. The notion that rare species are genetically depauperate in some fashion was led by G. Ledyard Stebbins as early as 1942. He suggested that without either within population or among population allelic diversity, rare species could not respond to selective pressures that may cause them to wink out. Also in the early 1940's, Stanley Cain (1940) suggested that some rarities lacked an ability to colonize new habitats because of a low genetic heterozygosity and consequently narrow ecological amplitudes.

Later notions about rarity dealt with mutational loads—i.e., rare species are somehow less fit because they bear deleterious alleles (Wright 1956; Huxley 1963). Thus, geneticists of the Modern Synthesis argued that rare taxa are doomed because of unfavorable genetic scenarios.

Evolutionary events. Concepts of rarity regarding the evolution of localized taxa suggested that these species might evolve rather suddenly. Three major ideas put forth by Californian botanists are central here. Saltational speciation through catastrophic selection is based upon the premise that, in a variable and fluctuating climate, occasionally an extreme reduction of population size in marginal populations may be associated with reorganization of the gene pool (Lewis 1962). Harlan Lewis, most famous for his work on *Delphinium* and *Clarkia*, suggested that such drastic fluctuations are characteristic of populations of many annual plants in California. Several years later, Peter Raven (1964) linked catastrophic selection with edaphic endemism for various members of *Clarkia*, as well as for *Navarretia*, *Hesperolinon*, and the *Streptanthus glandulosa* complex.

A second evolutionary theme involves the likelihood of mutational events leading to a new breeding system. Les Gottlieb (1973a) documented the evolution of the new, rare taxon, *Stephanomeria malheurensis* from its parent species, *S. exigua* ssp. *coronaria*, by a single mutational change. The rare *Stephanomeria* is a self-pollinating species, while the common and widespread *Stephanomeria* is an obligate outcrosser.

Third, the now classic contribution by G. Ledyard Stebbins and Jack Major (1965) examined endemism and speciation in the California flora by identifying the evolution of endemic taxa through chromosomal rearrangement. They cite a wealth of examples, illustrating that chromosomal evolution via changes in ploidy level has had a major role in the evolution of California's rarities.

TABLE 1. OLD IDEAS CONCERNING RARITY IN VASCULAR PLANT SPECIES, WITH THE MOST CURRENT THINKING ABOUT EACH TOPIC SUMMARIZED.

I. Age

1. Rare species are "old" species (Lyell 1830–1833; Darwin 1872; Fernald 1918, 1925, 1929, 1942, 1950)
2. Rare species are "new" species (Rafinesque 1836; Willis 1922)

Current Synthesis: Rare species are of all ages. No broad generalizations about age of rarity can or should be made.

II. Ecology

1. Rare species are habitat specialists (Watson 1845)
2. Rare species are poor competitors (Griggs 1940; Kruckeberg 1951)
3. Rare species result from the superimposition of diverse and unusual lithic features upon a wide range of climatic conditions (Mason 1946a, b)

Current Synthesis:

1. Rare species can be habitat specialists, but many are not. No broad generalizations can or should be made.
2. Rare species can be poor competitors, such as in the genus *Streptanthus*, but many are not. No broad generalizations can or should be made.
3. A large proportion of the rare species in California do result from the superimposition of diverse and unusual lithic features upon a wide range of climatic conditions—a feature of the California flora recognized for over a century.

III. Genetics

1. Rare species exhibit low genetic diversity (Cain 1940)
2. Rare species consist of one or very few biotypes (Stebbins 1942)
3. Rare species resulted from the accidental fixation of deleterious (or useless) mutations (Wright 1956; Huxley 1963)

Current Synthesis:

1. Rare species can have low genetic diversity, but there are a number of exceptions, any of which come from the California flora. No broad generalizations can or should be made.
2. Rare species can consist of one of very few "biotypes," but no broad generalizations can or should be made. We have few data.
3. Rare species theoretically may have resulted from the accidental fixation of deleterious (or useless) mutations, but we have no empirical data to support this hypothesis.

IV. Evolutionary Events

1. Rare species originate from catastrophic selection on rare or unusual substrates (Raven 1964)
2. Rare species originate from a mutation leading to a new breeding system (Gottlieb 1973)
3. Rare (endemic) species originate through chromosomal rearrangement and the evolution of closely related taxa of different ploidy level (Stebbins and Major 1965)

Current Synthesis:

1. Rare species can originate from catastrophic selection on rare or unusual substrates, as in the genus *Clarkia*, but these data are hard to obtain. No broad generalizations can or should be made.
2. Rare species originate from a mutation leading to a new breeding system, as in the genus *Stephanomeria*, but these data are hard to obtain. No broad generalizations can or should be made.
3. Rare (endemic) species do originate through chromosomal rearrangement and

TABLE 1. CONTINUED

the evolution of closely related taxa of different ploidy level, and this was documented extensively by Stebbins and Major. However, this is not true in a universal sense, and no broad generalizations can or should be made.

V. Synthetic Approaches

1. Rare species are:
 - (a) particularly susceptible to environmental stochasticities,
 - (b) less competitive, and
 - (c) less plastic in their ability to respond to new selection pressures (Darwin 1872)
2. Rare species result from the interaction of:
 - (a) a unique, localized environment,
 - (b) a specific genetic structure of each population, and
 - (c) a past evolutionary history peculiar to each taxon (Stebbins 1980: "Gene Pool-Niche Interaction Theory")

Current Synthesis: True, but not in a universal sense. No broad generalizations can or should be made.

Synthetic approaches. Darwin (1872) proposed that rare species are particularly susceptible to environmental stochasticities, less competitive, and less plastic in their ability to respond to new selection pressures (Darwin 1872). Although we cannot generalize as yet about multiple causes of rarity, his perspicacity presages our own, seemingly clumsy efforts to erect monothetic theories of cause.

One hundred years later, Stebbins (1980) put forth the gene pool/niche interaction theory, suggesting that rare species result from the interaction of a unique, localized environment, a specific genetic structure of each population, and a past evolutionary history peculiar to each taxon. The synthesis is very useful because we have come to realize that rare species are unlikely to be rare for any one single reason.

NEW IDEAS ABOUT RARITY

The new ideas about the causes of rarity presented below are really an update of what we think about these old ideas today. Table 1 summarizes the commentary below.

Age. In California, we have many old species or paleoendemics, probably the most famous are the redwoods *Sequoia sempervirens* and *Sequoiadendron giganteum*. From the fossil record we know that during middle Tertiary, the exceptionally rich mixed conifer

and subalpine forests of which these species were a part, shifted coastward as the cooling and drying trend accelerated (Raven and Axelrod 1978). Areas occupied by *Sequoia* and *Sequoiadendron* during the Tertiary were mutually exclusive as they are today. The more widely distributed genus *Sequoia* occurs farther north and coastward, inhabiting in a region of moister, milder climates. But there are other rare paleoendemics, such as *Lyonothamnus floribunda* and *Romneya coulteri*, with doubtless wider ranges in the Tertiary (Raven and Axelrod 1978). These taxa are now restricted to the relatively mild climates in California.

The age of other rare species is harder to ascertain, primarily because of an absence of rare plant fossils in the geologic record. Botanists must resort to correlative data, such as the geologic age of a specific habitat with the habitat specificity of a taxon. For example, Beal and Ownbey (1943) suggested that the rare triploid variety of *Calochortus longebarbatus*, *C. l.* var. *peckii*, endemic to the Ochoco Mountains of Central Oregon, is at least one million years old. These arguments were based on poor dispersal ability of the mariposa lily and the age of geological formation in which this mariposa lily is found.

New species, neoendemics, are represented by many examples in the California flora. It is generally accepted that most of California's endemics are new species (Stebbins 1978b). Most of these rarities are annual species, and are found in some more familiar genera, such as *Downingia*, *Eriogonum*, *Lasthenia*, *Limnanthes*, and *Linanthus*. *Eriogonum* is a particularly instructive genus. Skinner and Pavlik (1994) list 71 (approximately 36%) rare *Eriogonum* taxa in California, many of which are annual species.

Still other rare species may not be so old, or more importantly, their age is irrelevant in explaining causes of rarity. I suspect that many rare members of the Scrophulariaceae, such as *Castilleja affinis* ssp. *neglecta*, for example, are not particularly old or new. We simply lack evidence to invoke age as a reason for their limited distribution and abundance.

Ecology. What do we know about habitat specialists and about the competitive abilities of rare taxa? To answer the first question, we now know that many of our rarities in California are habitat specialists. This supports precisely what Herbert Mason suggested nearly fifty years ago—that California has a diversity in climate, topography, and soil type that is rivaled by almost nowhere else in the world. Although Mason (1946a, b) discussed at length our ultramafic endemic taxa, four additional examples illustrate the complexity of this phenomenon.

Brodiaea pallida is found in one extended population on vernal streambeds on serpentinite substrates in one small area of Tulare

County. It is threatened with development, and with possibly hybridization with *B. elegans*, a more common and widespread species. Thus its habitat requirements include a specific seasonal moisture regime on a very specific soil type in a very specific climatic zone. *Lilaeopsis masonii* is restricted to the littoral zone (splash zone) of Sacramento-San Joaquin Delta and Napa River. Its elevational range is only a few feet, and its primary habitat can be described as the ephemeral and precarious Delta shoreline that is subject to daily inundation by tidal action.

Calochortus striatus is a rare lily restricted to the vernally moist springs and meadows of the Mojave Desert, and *Oenothera deltoides* ssp. *howellii* is known from only seven populations in the rare and remnant aeolian sand deposits along the western edge of the San Joaquin River. These latter two species occur on ancient, remnant habitats characteristic of a time now past.

The second major ecological theory for rare plant species suggests that they are poor competitors. An interesting California example is the rare *Raillardiopsis muirii*—a species that provides several lessons about rarity in the California flora. This taxon has an extraordinary biogeographic history, as it is widely disjunct between the Ventana Double Cone in the Santa Lucia Range, and in the southern Sierra Nevada from Fresno to Kern County. Although the southern Sierra Nevada populations are nearly restricted to the Kings and Kaweah River drainages, there are three significant outlying populations—Baker Point, Church Dome, and Owens Peak. Baldwin and Kyhos (1990) proposed that this modest composite is 5 million years old, and represents the ancestral sister group to the Hawaiian tarweeds—a modest dispersal event (for a self-incompatible species) of over 3500 km. In addition to being a habitat specialist of considerable antiquity, it has been suggested that *Raillardiopsis muirii* may also be a poor competitor, being restricted to rather bare granitic substrates because it cannot compete successfully elsewhere.

Genetics. The genetics of rare species is a controversial topic, possibly because no consensus exists about the level of heterozygosity that characterizes rare plant taxa. In a recent review Hamrick et al. (1991) documented that endemic species, as representatives of rare taxa, have less than half the genetic diversity of widespread species. Narrowly and regionally distributed species have intermediate values. These documented differences in genetic diversity between endemic and widespread species are due largely to differences in the proportion of gene loci that are polymorphic (Hamrick et al. 1991). In addition, widespread species have more alleles at polymorphic loci than do endemic species.

There are many famous rarities in the botanical world that have little or no detectable genetic variation, such as *Pedicularis furbishiae*

(Waller et al. 1987), *Howellia aquatilis* (Lesica et al. 1988), and *Oenothera organensis* (Levin et al. 1979). California examples are also often cited, such as *Clarkia franciscana* and *Pinus torreyana*. But California also leads in the number of documented exceptions to this rule, as measured by percentage of gene loci that are polymorphic. For example, *Pinus longaeva* shows moderate to high amounts of polymorphism (79%, Hiebert and Hamrick 1983), *Layia discoidea* is highly polymorphic (19 of 21 gene loci surveyed; Gottlieb et al. 1985); as is *Limnanthes bakeri* (39% of loci are polymorphic, Kesseli and Jain 1984); and *Dedeckera eurekaensis* (77–89% of loci are polymorphic, varies with population; Weins et al. 1989). Nearly fifteen years after Stebbins (1980:80) concluded that “there appears to be no recognizable correlation, either positive or negative, between the amount of genetic variation within populations of plant species and the rarity or commonness of the species as a whole,” we cannot prove otherwise.

Finally, Wright's (1956) suggestion that rare species carry a high genetic load may be borne out in the rare paleoendemic shrub *Dedeckera eurekaensis*. Wiens and his colleagues (1989) found that less than 0.5% of the seeds of *Dedeckera eurekaensis* are fully viable, and they suggest that this ancient taxon persists as rare, multiple-locus heterotic genotypes that have a low reproductive potential because of an excessively high segregational genetic load.

Evolutionary events. The genus *Clarkia* has presented California's systematicists, along with her geneticists and ecologists, a wealth of questions about the evolution of rare forms. As mentioned previously, saltational speciation through catastrophic selection was developed by Harlan Lewis, in large part to illustrate the evolution of rare species of *Clarkia*. Although originally described for the derivation of *Clarkia franciscana* from *C. rubicunda*, Gottlieb (1973b) has shown that the former species is probably not derived in as direct a fashion as originally conceived by Lewis. However, this evolutionary mode of origin is likely to be true for other species of *Clarkia*, including *C. exilis* (Vasek 1958), *C. springvillensis*, *C. temblorensis*, and *C. caliente* from the widespread parental species *C. unguiculata* (Vasek 1971; Lewis 1973). The rare *Clarkia* species appear to evolve in progressive adaptation to increasing aridity, and all are accompanied by aneuploid changes in chromosome number, allopolyploidy, and autogamy (see Raven and Axelrod 1978 for a concise discussion of *Clarkia* evolution).

Synthetic approaches. The most useful approaches to understanding rarity in vascular plants is clearly one that takes a pluralistic approach. Rarity is not a monothetic phenomenon, but usually the congruence of several events. Perhaps the most useful descriptive synthetic approach is the one proposed by Rabinowitz (1981) and

Geographic Range	Large		Small	
Habitat Specificity	Wide	Narrow	Wide	Narrow
	Widespread Taxa	Predictable Taxa	Unlikely Endemic Taxa	Endemic Taxa
Large, Dominant, Local Populations	Common Plants - <i>Allium validum</i>	<i>Calochortus striatus</i>	<i>Allium munzii</i>	<i>Calochortus tiburonensis</i>
Small, Non-dominant, Local populations	Sparse Plants - <i>Muilla coronata</i>	<i>Nolina interrata</i>	Non-Existent?	<i>Brodiaea pallida</i>

FIG. 1. Seven forms of rarity (Rabinowitz 1981), as illustrated by various members of the California Liliaceae.

her students and colleagues, whose work on rare/common differences has inspired many of us to organize our thoughts about consequences of rarity (Rabinowitz 1978; Rabinowitz et al. 1979, 1984, 1989; Rabinowitz and Rapp 1981). Rabinowitz suggested that there are seven forms of rarity, as defined by geographic distribution, population size, and habitat specificity (Rabinowitz 1981). Floras or even taxonomic groups (Fig. 1) can be organized to provide insight into the types of rarities in a geographic region or phylogenetic context.

With respect to the synthetic approaches suggested by Darwin (1872) and Stebbins (1980), we know that evolutionary history, genetics, and habitat preferences explain the distribution of many taxa, both rare and common. And while these represent only three of the many variables that may explain rarity, synthetic viewpoints do not necessarily lead to broad generalizations about the causes and consequences of rarity.

A LOOK TO THE FUTURE

Bruce Pavlik and his students and colleagues are leading the way in rare plant biology today. They are clearly taking a synthetic approach, working experimentally to determine the causes of rarity in the exceedingly rare borage, *Amsinckia grandiflora* (Pavlik 1991a, b, 1992, in press). Pavlik's work demonstrates that careful, indeed elegant, experimental design can lead to definitive results explaining a rare plant's status.

Comparing rare and common congeners. One of the more fruitful approaches to understanding rarity is through the comparison of a rare taxon with a closely related common congener (e.g., Primack 1980; Karron 1987a, b, 1989). As mentioned before, Rabinowitz's work (Rabinowitz 1978; Rabinowitz et al. 1979, 1984, 1989; Ra-

binowitz and Rapp 1981) is seminal in this regard, as is the informative, but generally overlooked review by Babbel and Selander (1974). Two studies discussed below illustrate the utility of a comparative approach.

Recently, the reproductive biology of *Amsinckia grandiflora* was compared to that of the widespread *A. menziesii* var. *intermedia* (Pantone et al. in press). *Amsinckia grandiflora* is known from only three natural populations while *A. menziesii* var. *intermedia* is a widespread, rather aggressive weed across the semiarid western U.S. Interestingly, *A. menziesii* var. *intermedia* is increasing its range as this species establishes successfully in Australia, Europe, New Zealand, and South Africa (Pantone et al. in press). The two *Amsinckia* taxa have similar physiologies, morphologies, and phenologies, but they differ rather dramatically in their breeding system. *Amsinckia grandiflora* is heterostylous with probable seed abortion in flowers pollinated by the same floral morph, while *A. menziesii* var. *intermedia* is homostylous and self-fertile.

In the study, Pantone et al. (in press) documented that the differences in reproductive biology of the rare and common species, as determined by various measures of seed and inflorescence production, suggest that the homostylous weedy congener has overcome the intrinsic limits on fecundity set by heterostyly in its rare congener. Thus the constraints of a very specific breeding system dictate the intrinsic cause of rarity in *Amsinckia grandiflora*, and further limits to the successful seedling establishment and reproduction of this rare annual borage are imposed by the exotic grass species now naturalized within *Amsinckia*'s grassland habitat (Pavlik 1991a, b, 1992).

A number of years ago I documented reproductive differences among populations of rare species, and between populations of rare and common species of *Calochortus* (Fiedler 1987). The common species, *C. albus*, was found to reproduce at a smaller bulb size, produce a greater mean number of flowers and fruits per individual, and exhibit a higher amount of vegetative reproduction, as compared to the rare species *C. obispoensis* and *C. tiburonensis*, but not to *C. pulchellus*. In addition, the reproductive efforts appeared "chaotic" in the technical sense (Vandermeer 1982), and therefore gave credence to the suggestion that the population dynamics of rare species are chaotic. Finally, the common species also had a greater probability of survival to reproductive maturity, thereby increasing its reproductive success relative to the rare congeners (Fiedler 1987). However, despite these autecological life history differences, all populations of both rare and common species appeared to be, at the very least, stable or increasing in numbers, using a Leslie matrix approach (Fiedler 1987). I concluded that it is difficult to generalize about the life history or population dynamics for a rare species within

a single genus, and this admission diminishes a broader generalization about the behavior of rare plants.

"Perhaps the most significant aspect of this work is the conclusion that rare species may be idiosyncratic, *i.e.*, each rare species exhibits a host of individual and populational differences that distinguish it not only from more common species, also from other rare congeners." (Fiedler 1987:993).

Anthropogenic vs. natural rarities. The preceeding discussion has focused on natural rarities, or those species that are rare due solely to their biology, evolutionary history, or both. Anthropogenic rarities, however, are species that may or may not be rare due to the biology or evolutionary history, but currently are rare because of the negative impact interactions with humans have had on their populations (Fiedler and Ahouse 1992). They are not wholly distinct categories, however, as anthropogenic rarities may also begin as natural ones.

We can look to the new California Native Plant Society Inventory of Rare and Endangered Vascular Plants of California (Skinner and Pavlik 1994) to determine the proportion of rare taxa that are largely considered anthropogenic rarities. In the last five years since the previous edition (Smith and Berg 1988), the editors identified an additional 313 new rare and endangered plants (Table 2). Skinner and Pavlik (1994) suggest four reasons why there is such a increase.

- (1) Taxonomic changes have identified new rarities (7%). This nomenclatural shuffling is to be expected, and we shall always have a small percentage of rarities appear as our floras are updated.
- (2) Rare plants have been overlooked in the past. Approximately 63% of the 182 newly listed taxa in the 5th edition were not listed in previous editions because they were overlooked. This is extraordinary, largely because of the long history of intensive botanical surveys in California and the western United States (Ertter 1995), and because of California's well-known efforts to conserve its rare flora.
- (3) Many new plants (15%) have been described in California. This is wonderful news, and gives us confidence that competent and still inquisitive botanists are still working on the complexities of California's flora.
- (4) More plants (32%) are becoming endangered as habitat loss and other threats accelerate. This is troublesome, particularly with the recent predictions of staggering population increases for California in the coming century. These are the anthropogenic rarities to which we must turn in our protection efforts.

TABLE 2. PERCENTAGE OF FOURTH EDITION TAXA ON EACH LIST COMPARED TO THE NUMBER AND PERCENTAGE OF NEW FIFTH EDITION TAXA ON EACH LIST (SOURCE: SKINNER, M. W., AND B. M. PAVLIK, 1994).

CNPS list	% 4th Edition	Taxa new to 5th Edition	% new taxa
1A. Presumed Extinct in California	3%	3	1%
1B. Rare or Endangered in California & Elsewhere	44%	136	43%
2. R/E in California, More Common Elsewhere	11%	82	26%
3. Need More Information	10%	12	4%
4. Plants of Limited Distribution	33%	80	26%
Total	100%	313	100%

I predict that we will be focusing our conservation efforts more on the last of these rarities—i.e., anthropogenic rarities. I suggest further that this phenomenon is problematic, because knowing that they are anthropogenic rarities (and not, for example, competitively constrained) will provide little predictive power for preventing their populations from becoming extinct. The idiosyncratic nature of the taxa will become increasingly clear. Although we can separate causes of rarity from their consequences, in the case of anthropogenic rarities we must start with basic research on their autecology, without much theoretical power to guide our initial efforts.

CONCLUSIONS

In some fortunate instances, such as at the Eureka dunes, Inyo County, rare plant taxa, such as *Swallenia alexandrae* and *Oenothera avita* ssp. *eurekensis*, are more threatened by human disturbance, pollinator availability, and climatic fluctuations than by any intrinsic life history characteristic (Pavlik and Barbour 1988). These rare plants are spectacular examples of the California flora that are relatively secure. Such instances are relatively rare.

More disturbing are examples like *Lasthenia maritima* and *L. minor*. The former species is a rare composite restricted to the seabird islands along the coast of the Pacific Northwest, while the latter species, *L. maritima*'s progenitor, is not listed as rare, but is rapidly becoming rarer because of habitat destruction and degradation. The formerly common species may be more likely to go extinct than the naturally rare neoendemic.

Finally, we should not focus all our conservation efforts on our designated rarities, but instead, focus also on the protection of the rarest of things—e.g., individual or populational expressions of rare color forms, unusual morphologies, and rare genetic events. If we

do not redirect some of our management efforts toward these rarities, I suspect that we will lose much of the evolutionary theatre of California's magnificent flora, and that the period of rapid evolution of the majority of our rare species will have seen the final curtain.

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(Received 11 Jul 1994; accepted 3 Feb 1995)

FLOWERS IN THE GARDEN: WHAT NEXT FOR CALIFORNIA FLORISTICS?

DIETER H. WILKEN
Santa Barbara Botanic Garden,
1212 Mission Canyon Road, Santa Barbara, CA 93105

ABSTRACT

As much as 79.5% of the California Floristic Province and 73% of the State of California remains poorly inventoried, judging from a review of local and regional floras. The Cascade Range, the Sierra Nevada, the Great Valley, and the Modoc Plateau have been especially neglected. The southern Sierra Nevada, portions of the Diablo Range, the Warner Mountains, the Little San Bernardino Mountains, and most of the major mountain ranges of northwestern California merit special attention. Most local and regional floras have been descriptive. Detailed and informative analyses of floristic patterns and processes depend on fine-scale samples of phytogeographic and floristic regions. Future studies should include comparative analyses, using appropriate exploratory statistical methods that examine overall relationships. Such approaches may reveal patterns deserving further inquiry. Studies of biogeographic processes (that have shaped California's flora) and local or regional patterns of diversity will benefit from new approaches that include molecular analyses and application of cladistic methods.

The California flora is well known for its species diversity and endemism (Raven and Axelrod 1978; Stebbins and Major 1965). Much of this diversity is coincidental with political boundaries superimposed on a natural phytogeographic region, the California Floristic Province (Howell 1957). The province is characterized by a Mediterranean climate, considerable topographic and geologic diversity, and a geochronological history that involved elements of the Arcto-Tertiary and Madro-Tertiary Geofloras (Raven and Axelrod 1978).

The first statewide vascular flora of California (Brewer et al. 1876; Watson 1880) resulted from William Brewer's participation in the Geological Survey of California (Farquhar 1949). The 2-volume "Botany" of the Survey was supplanted by Jepson's *A Flora of California* (Jepson 1909–1943; Dempster 1979), which included identification keys, morphological descriptions, ecological and geographic distributions, citation of synonyms and specimens, and discussions of taxonomic affinities. Jepson (1925) and subsequent regional or statewide treatments (Abrams 1940–1951; Ferris 1960; Hickman 1993; Mason 1957; Munz 1974; Munz and Keck 1968) were primarily designed for brevity and identification purposes. Consequently, the difference in information content between Jepson's flora

and subsequent statewide treatments (perhaps best called manuals, *fide* Lawrence 1951) is a function of scale. Because detailed analyses of floristic patterns (and their relationship to abiotic and biotic processes) depend on specimen-based data sets (Pielou 1979; Myers and Giller 1988), floras are more informative than manuals. Unfortunately, economics of field and herbarium studies often restrict the size of floristic studies. Floras based on political boundaries present an analogous problem, because they rarely coincide with natural physiographic units.

Since the mid-19th century, California's flora has received much attention from systematic, ecological, and geographic perspectives. The purpose of this paper is to review progress in the inventory of California's flora, relative to geographic distribution. I restricted my review to published scientific studies in which (1) authors claimed systematic sampling techniques throughout their study areas and (2) voucher specimens and herbarium repositories were clearly cited. The survey was confined to the years 1960–1993, which represent 34 years of published work subsequent to Munz and Keck (1959). Unpublished theses, reports by local government agencies, reports by environmental consultants, and other literature not readily in the public domain were excluded. Some earlier literature citations were added retrospectively for purposes of discussion. Descriptive studies of vegetation were excluded, because published data are often restricted to species occurring above a specified frequency. An informative and more extensive list of references for the California flora (including many unpublished reports and theses) can be found in Smith (1992).

I arranged floras by classifying them in the hierarchical system used in *The Jepson Manual* (Hickman 1993), which recognizes 3 floristic provinces and 10 major subdivisions. Because these categories more closely approximate natural physiographic units (Fenneman 1931) than political units (e.g., counties), they are more informative for purposes of floristic comparison. I was unable to accurately estimate areas of subdivisions directly, but they sufficiently coincide with the 10 floristic regions of Raven and Axelrod (1978) so as to permit a general estimate of area in km². I extracted area estimates from floras in Table 1 and calculated their combined proportion of floristic regions, after correcting for overlap. My estimates for the Sierra Nevada, the Great Valley, Central Western California, and Southwestern California should be used with caution, because I was unable to clearly define subdivision boundaries within several politically defined floras (e.g., Hoover 1970; Twisselmann 1967). I also surveyed literature from 1978–1993, using Raven and Axelrod (1978) as a benchmark, for synthetic analyses of patterns at local and regional levels.

Table 1 includes 73 references pertaining to 63 local or regional

TABLE 1. CLASSIFICATION OF 73 REFERENCES PERTAINING TO 63 LOCAL OR REGIONAL FLORAS OF CALIFORNIA. Numbers in () or [] are km². Numbers in [] represent sums of estimates from references/total area for each province or subdivision. Numbers in () represent estimates of individual references. ^a Combined area of 9085 km² for North Coast and North Coast Ranges was obtained from Smith and Wheeler 1990–1991. ^b 2000 km² was estimated for the 3 subdivisions of Sierra Nevada from parts of Twisselmann 1967 (21,165). ^c 6000 km² was estimated from parts of Hoover 1970 (5800), Twisselmann 1967 (21,165), and Smith 1976 (5600). ^d 27,570 km² was estimated from parts of Hoover 1970 (5800), Howell 1970 (1370), Thomas 1961 (3590), Howitt and Howell 1964, 1973 (8610), Smith 1976 (5600), and Twisselmann 1956 (7050), 1967 (21,165). ^e 13,050 km² was estimated from parts of Beauchamp 1986 (10,935), Boughey 1968 (1800), Fletcher 1983 (57), Raven et al. 1986 (985), Smith 1976 (5600) and Twisselmann 1967 (21,165). ^f 6800 km² was estimated from parts of Beauchamp 1986 (10,935) and Twisselmann 1967 (21,265).

California Floristic Province [66,850/324,000]

Northwestern California [9630/55,000]

North Coast: Hardham and True 1972 (4); Hektner and Foin 1977 (7); Smith and Wheeler 1990–1991^a.

Klamath Ranges: Ferlatte 1974 (455).

North Coast Ranges: Heckard and Hickman 1985 (55); King 1985 (2.5); Murphy and Heady 1983 (21); Smith and Wheeler 1990–1991^a.

Cascade Ranges [780/34,370]

Cascade Range Foothills: No references.

High Cascade Range: Cooke 1940, 1941, 1949 (260); Gillett et al. 1961 (520).

Sierra Nevada [3131/43,380]

Sierra Nevada Foothills: Jockerst 1983 (7); Twisselmann 1967^b.

High Sierra Nevada: Smiley 1921 (area not estimated); Hunter and Johnson 1983 (60); Knight et al. 1970 (13); Lavin 1983 (500); Palmer et al. 1983 (80); Savage 1973 (50); Smith 1973, 1983 (480); Twisselmann 1967^b; Howald 1981 (1).

Tehachapi: Twisselmann 1967^b.

Great Valley [6012.5/59,390]

Sacramento Valley: Broyles 1987 (5); Jockerst 1983 (7); Schlising and Sanders 1983 (0.5).

San Joaquin Valley: Twisselmann 1956, 1967^c; Hoover 1970 and Keil et al. 1985^c; Smith 1976^c.

Central Western California [31,750/47,920]

Central Coast: Barbour 1970, 1972 (6.5); Coulter 1970, 1978 (0.5); Fletcher 1983 (57); Genetti and Engles 1984 (15); Howell et al. 1958 (115); Howell 1970^d; McClintock et al. 1990 (12); Peñalosa 1963 (15); Thomas 1961^a.

San Francisco Bay Area: Bowerman 1944 (142.5); Howell 1970^d; Ripley 1980 (8); Shar smith 1945 (3885); Thomas 1961^d; Howitt and Howell 1964^d, 1973; Wetzel 1971 (10).

South Coast Ranges: Bickford and Rich 1984 (15.5); Ferren et al. 1984 (4); Fletcher 1983 (57); Genetti and Engles 1984 (15); Griffin 1974 (7.5); Hoover 1970^d and Keil et al. 1985; Howitt and Howell 1964^d, 1973; Smith 1976^d; Twisselmann 1956, 1967^d.

Southwestern California [15,550/47,500]

South Coast: Boughey 1968^e; Ferren 1985 (1); Fletcher 1983^e; Raven et al. 1986^e; Smith 1976^e; Beauchamp 1986^e.

Channel Islands: Junak et al. 1995 (249); Philbrick 1972 (2.6) and Junak et al. 1993; Raven 1963 (145); Thorne 1967, 1969 (194); Wallace 1985 (904).

TABLE 1. CONTINUED

Transverse Ranges: Magney 1986 (4); Smith 1976 ^c ; Twisselmann 1967 ^c .
Peninsular Ranges: Boughey 1968 ^c ; Beauchamp 1986 ^c ;
Lathrop and Thorne 1978 (1150), 1983 (0.5), 1985 (181).
Great Basin Floristic Province [3037/22,600]
Modoc Plateau: Applegate 1938 (225).
East of Sierra Nevada: Forbes et al. 1988 (31); Howald and Orr 1981 (1);
Lavin 1983 (500); Lloyd and Mitchell 1973 (2280)
and Morefield et al. 1988.
Desert Floristic Province [42,191/87,180]
Mojave Desert: DeDecker 1984 (30,000; Castagnoli et al. 1983;
Hart et al. 1979; Pavlik 1985 (50); Peterson 1986 (1066);
Thorne et al. 1981 (3291); Twisselmann 1967 ^r .
Sonoran Desert: Beauchamp 1986 ^c ; McLaughlin et al. 1987 (2050).

floras. California has an area of 411,000 km² (Raven and Axelrod 1978). After correction for overlap, the area covered by floras in Table 1 was estimated to be 112,080 km², representing 27% of the state's area. The area of the California Floristic Province, which includes small portions of Oregon and Baja California, is 324,000 km² (Raven and Axelrod 1978). The area of this province covered by floras in Table 1, after correction for overlap and excluding those covering the Great Basin and Desert Provinces, was estimated to be 66,850 km² (20.6% of the Province).

Northwestern California is represented by 7 floras, covering 17.5% of the subdivision's area. Studies of the Trinity Alps (Ferlatte 1974) and Snow Mountain (Heckard and Hickman 1984, 1985) are notable for their analyses of floristic affinities. Several important physiographic units, including the Siskiyou and Yolla Bolly Ranges, have not been systematically surveyed, although 6 unpublished theses were cited by Smith and Sawyer (1988).

The Cascade Ranges are represented by only 2 floras, covering 2.3% of the subdivision's area (Cooke 1940–1977; Gillett et al. 1961). The recent discovery of *Neviusia* (Shevock et al. 1992) clearly suggests that this region deserves special attention.

Surprisingly, the Sierra Nevada does not appear adequately represented. Only 10 floras, covering 9% of the subdivision's area, have surveyed this most prominent feature of California's landscape. Four of them treated relatively small but natural physiographic units (Jokerst 1983; Palmer et al. 1983; Savage 1973; Smith 1973, 1983) in the northern Sierra Nevada. Twisselmann (1967) covered the southern Sierra Nevada and Tehachapi Mountains of Kern County. Smiley's (1921) study, whose area was not determined, represents a notable, early attempt to analyze origins and relationships of the higher elevation flora. Shevock (1988) presents a strong case for further inventories.

The flora of the Great Valley is poorly documented, with 6 floras covering 10% of the subdivision's area. Most of the inventoried area is represented by the southern San Joaquin Valley (Hoover 1970; Twisselmann 1956, 1967; supplemented by Keil et al. 1985). Unfortunately, because of agriculture and urbanization, a synthesis of the Great Valley flora will have to be based primarily on historic herbarium records and studies of small, undeveloped areas.

Central Western California, perhaps the best studied region in California, is treated by 26 references that cover 66% of the subdivision's area. The Diablo Range between Pacheco Pass and the Temblor Range (between Sharsmith 1945 and Twisselmann 1956) is a major physiographic unit remaining to be inventoried. The flora of the Santa Lucia Range needs synthesis, although parts are covered in at least 3 references (Hoover 1970; Howitt and Howell 1964, 1973).

Fifteen floras, based on 17 references, cover 33% of Southwestern California. Although most of the western Transverse Ranges are treated by relatively recent floras (Raven et al. 1986; Smith 1976; Magney 1986; Twisselmann 1967), floras of the eastern Transverse Ranges (San Gabriel and San Bernardino Mountains) have not been reviewed and updated since Parish (1917–1918). The San Jacinto Mountains, in the Peninsular Ranges, were last treated by Hall (1901). The contiguous Santa Rosa Mountains apparently remain to be systematically surveyed. Wallace (1985) provided a thorough checklist for all California islands based on selected specimens. Smith (1976) included the four northern Channel Islands. Only San Clemente, Santa Catalina, Santa Barbara, and Santa Cruz islands have published floras based on extensive field studies. Because of urbanization, a thorough floristic inventory of the lower Los Angeles, San Gabriel, and Santa Ana River drainages will depend almost exclusively on historic herbarium collections.

Six floras cover 13.5% of the Great Basin Province, but the White Mountains (Lloyd and Mitchell 1973; Morefield et al. 1988) contribute to most of the estimate. The best documented flora for the Modoc Plateau region appears to be Applegate (1938), supplemented partly by Smith et al. (1993). Although the floristic boundary between the Modoc Plateau and the Cascade Range is unclear (Hickman 1993), the Warner Mountains clearly represent a distinct physiographic unit, floristically related to Great Basin ranges, and apparently unstudied (Raven and Axelrod 1978).

The Desert Province of Hickman (1993) is composed of only 2 subdivisions, but includes 3 distinct floristic regions, the Inyo, Mojave, and Colorado (Stebbins and Major 1965; Raven and Axelrod 1978). Hickman's Mojave subdivision (which approximates the Inyo and Mojave regions) is treated by 5 floras that cover as much as 38,000 km² (66% of 57,730 km²). However, much of the region

covered by DeDecker (1984) has been incompletely sampled; exclusion of her treatment, but including Peterson (1986), reduces the estimate to 9,100 km² (16%). No flora has been published for the Little San Bernardino Mountains, which are contiguous to 3 California floristic provinces (Raven and Axelrod 1978). The Sonoran Desert subdivision (Colorado region) is treated by only 2 floras (4,250 km² or 15% of area), and no flora exists for most mountain ranges and intervening basins of eastern Riverside and Imperial Counties and southeastern San Bernardino County.

Most floras in Table 1 are descriptive but some discuss floristic affinities in general terms or address particular species assemblages. Notably, Peterson (1986) used Jaccard's Coefficient (Sneath and Sokal 1973) to determine patterns of overall floristic similarity among 12 desert mountain ranges, based on several unpublished reports and theses. This coefficient is limited in its application to floristic data, but represents a useful exploratory tool for further analysis. McLaughlin (1986) investigated 50 local floras using factor analysis, which revealed objective circumscriptions of 7 floristic "elements" in the southwest. Raven (1967) analyzed the relationship between area and species number for Channel Island floras, based on migration and extinction equilibria (MacArthur and Wilson 1967). This approach, also used by Harper et al. (1978) to analyze relationships among 15 insular, montane floras of the Great Basin, represents a model for discussion of dispersal patterns and other factors that may influence floristic composition. These kinds of statistical methods provide effective and repeatable methods for analyzing the affinities of floristic regions at several levels of geographic scale.

Most synthetic analyses since Raven and Axelrod (1978) have focused on regional endemism (Axelrod 1982; Philbrick 1980; Smith and Sawyer 1988), with special attention to serpentine substrates (Kruckeberg 1984) and vernal pools (Jain 1976). Richerson and Lum (1980) examined relationships among species richness, climate, and topography. A few studies have tabulated distribution of life forms (Peterson 1986; McLaughlin 1986), but comparative studies are few, despite their importance to understanding dispersal and habitat requirements (Stebbins 1982). Some studies discussed hypotheses concerning the migration and origin of species comprising local and regional floras (Heckard and Hickman 1984; Stebbins 1982). Molecular analyses offer considerable promise in analyzing such problems, as exemplified by cpDNA restriction site variation among disjunct races of *Tolmiea* and *Tellima* in glacial refugia of the Pacific Northwest (Soltis et al. 1989, 1991). Such analyses, complemented by area cladograms (Mickevich 1981), may contribute to understanding some of California's floristic complexity.

Like the living collections found in botanic gardens, manuals for plant identification only provide limited views of the natural vari-

ation, ecological and geographic distribution, and evolutionary relationships among native and naturalized plant taxa. Significant progress in the study of the California flora will depend on inventories of current herbarium collections, systematic sampling of poorly known geographic areas, refined methods of analyses, and publication of results in accessible media. Detailed and informative analyses of floristic patterns and processes depend on fine-scale samples of phytogeographic and floristic regions. Such analyses will continue to rely on local and regional floras using specimen-based data sets. Judging from citations in Smith (1992), much can be accomplished by extracting data from unpublished documents. However, future floristic studies and analyses, including citation of voucher specimens, can and should be made more accessible through printed or electronic media.

ACKNOWLEDGMENTS

I deeply appreciate thoughtful reviews by Grady Webster and Bob Haller, whose comments helped improve the contents of this paper.

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(Received 28 Sep 1994; accepted 3 Feb 1995)

A NEW PROSPECT FOR CALIFORNIA BOTANY: INTEGRATING BIOSYSTEMATICS AND PHYLOGENETICS

BRUCE G. BALDWIN

Jepson Herbarium and Department of Integrative Biology,
University of California, Berkeley, CA 94720-2465

ABSTRACT

Integration of biosystematics (experimental study of biological aspects of organismal variation, diversity, and diversification) and phylogenetics (study of genealogical relationships of organisms) is a particularly promising avenue for future evolutionary and ecological investigations of the California flora. The exceptionally strong tradition of biosystematics in California botany has yielded findings that are responsible for much of our understanding of evolutionary processes in plants. The value of this research is, in part, attributable to a focus on the endemic plant lineages of California, which have provided ideal systems for investigating diverse modes of speciation and other evolutionary phenomena. An exciting new challenge to California botanists is reanalysis of biosystematic data and conclusions from a phylogenetic perspective. With understanding of phylogeny comes clarification of historical patterns and directionality of evolutionary changes and provision of more meaningful contexts for evolutionary comparisons. Phylogenetic research has indeed improved our understanding of speciation patterns, processes of diversification, and biogeographic relationships within California plant groups that were the subjects of earlier experimental studies. Only a small fraction of the California flora has been investigated from both biosystematic and phylogenetic perspectives.

Plant biosystematics, as defined here, is the experimental study of biological phenomena that are important for understanding plant variation, diversity, and diversification (see Grant 1984). Biosystematic studies include, for example, investigations of breeding systems, pollination biology, crossability and fertility relationships, chromosome evolution, niche relationships, and genetic and environmental components of phenotypic expression. In general, these types of studies involve some degree of experimental manipulation of living plants, such as crossing or transplanting. In contrast, phylogenetics is an analytical approach for reconstructing organismal genealogies (see Mishler this volume). Phylogenetic studies can be based on strictly descriptive data, usually from morphology or macromolecules; most systematic studies involving DNA sequences may be better classified as descriptive rather than biosystematic. It is important to note, however, that phylogenetics can be applied to, and is especially informed by, experimental data. DNA studies in the systematics community at large and in the Jepson Herbarium in particular extend, but do not replace, the tradition of descriptive

research on morphology that remains a pillar of plant systematics and taxonomy. Molecular investigations, and phylogenetic studies in general, are new components of the "unending synthesis" in systematic botany (Constance 1964).

THE IMPORTANCE OF BIOSYSTEMATICS AND PHYLOGENETICS TO CALIFORNIA BOTANY

The richness of botanical diversity in herbaceous, particularly annual, groups amenable to in-depth experimental investigation has been a major factor in promoting biosystematic research in California. Most importantly, like other regions of the world with a Mediterranean climate, California contains an unusually high number of large, neoendemic lineages that are ideal, natural study systems for biosystematists interested in plant speciation and evolution. The ecological components of biosystematic research have proven especially critical to understanding California plant evolution. Extreme heterogeneity and dynamism of soils, climate, and topography in California have apparently been major stimuli to evolution in the flora, wherein diversification within plant lineages has often spanned highly contrasting environments (see Stebbins and Major 1965; Raven and Axelrod 1978).

An exceptional wealth of biosystematic data from many of our most characteristic groups of California plants has accumulated since the early part of this century. In fact, some of the first biosystematic studies undertaken in plants were those of such famous Californian botanists as Babcock, Hall, Stebbins, and the Clausen, Keck, and Hiesey team (e.g., Babcock and Hall 1924; Stebbins 1950; Clausen 1951). These pioneering scientists laid much of the foundation of biosystematics for an impressive succession of Californian plant researchers in the latter half of this century (reviewed in part by Raven and Axelrod 1978; Grant 1981).

In contrast to the strong tradition of biosystematics in California, few phylogenetic studies of California plants have been published. This lack of attention to phylogenetics in California botany is partly attributable to the recency of theoretical advances (Hennig 1966; see Mishler this volume) and technological innovations (see Hillis and Moritz 1990; Swofford 1993) that have made phylogenetic analysis feasible. Also, most plant phylogenetic studies have focused on groups that include economically important species (e.g., Palmer et al. 1983; Doyle et al. 1990; Wendel and Albert 1992) or on questions pertinent to understanding the broad-scale pattern of plant evolution and to refining higher-level classification (e.g., Jansen et al. 1990; Chase et al. 1993). Those phylogenetic studies that have addressed relationships within California plant lineages, however, have offered important new insights into evolution and biogeography of the flora.

A phylogenetic framework can greatly aid the interpretation of biosystematic data by offering insights into the directionality and sequence of changes in biological attributes (e.g., breeding systems, chromosome numbers or arrangements, edaphic restrictions), in some cases allowing unequivocal determination of ancestral and descendant character states (see Maddison and Maddison 1992). In addition, phylogenetics can clarify whether occurrences of a biological correlation in different species of a plant group, such as dioecy and fleshy propagules, have arisen repeatedly from another condition, and are therefore perhaps ecologically or developmentally significant, or have arisen once and are shared among species because of a shared common ancestry (e.g., Donoghue 1989).

Phylogenetic studies can also allow interpretation of unavoidably incomplete biosystematic data within a more comprehensive organismal context. For example, traditional cytogenetic investigations can be limited in taxonomic scope by certain biological obstacles (e.g., crossing barriers, failure of meiotic chromosomal association in hybrids, or hybrid inviability), but these limitations do not restrict the extent of species sampling in non-experimental phylogenetic studies. Phylogenetic results can thereby extend partial cytogenetic data by offering an expanded, directional perspective on chromosome evolution and the origin of breeding barriers within species lineages (e.g., Baldwin 1993, 1994).

EXAMPLES FROM THE CALIFORNIA FLORA

Phylogenetic studies can play a major role in advancing experimental research on the California flora by focusing biosystematic efforts on important, unforeseen relationships. One of the most prominent examples of this type comes from the phylogenetic work of Sytsma and Gottlieb (1986a, b) on *Clarkia* (Onagraceae). The genus *Clarkia* has been the subject of more extensive biosystematic investigation than any other genus of California plants. Research on *Clarkia*, primarily by Harlan Lewis and colleagues/students (e. g., Lewis 1973; Vasek and Weng 1989) and, more recently, by Les Gottlieb and associates (e.g., Gottlieb 1974, 1993), has generated a phenomenal amount of cytogenetic, isozymic, ecological, breeding system, and developmental data. Results from biosystematic investigations of *Clarkia* have, in turn, greatly influenced our understanding of plant evolution. Recent phylogenetic studies, based on chloroplast DNA (Sytsma and Gottlieb 1986a, b; Fig. 1) and nuclear ribosomal DNA sequences (Hahn et al. 1993), forced a rethinking of generic delimitations when the only species of *Heterogaura*, *H. heterandra*, was found to have been derived from within *Clarkia*. This finding prompted submergence of *Heterogaura* within *Clarkia* (Lewis and Raven 1992) and raised new questions about floral and

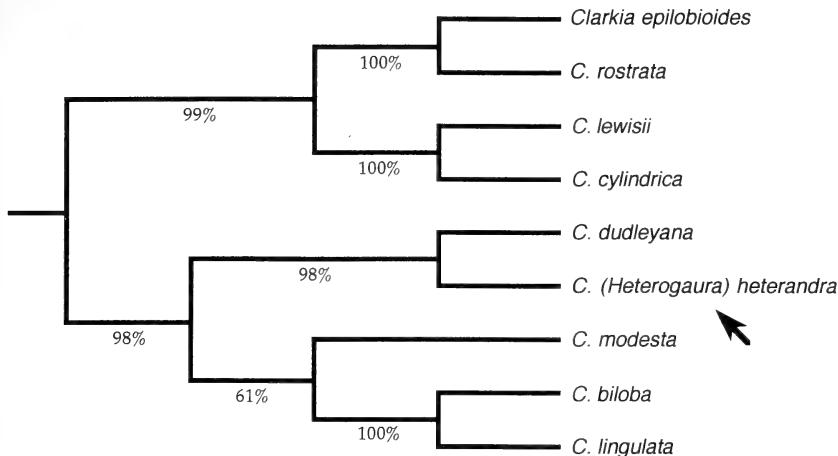


FIG. 1. Phylogenetic tree of *Clarkia* sect. *Peripetasma* (Onagraceae) based on chloroplast DNA restriction site mutations (redrawn from Sytsma and Gottlieb 1986a, b). Sytsma and Gottlieb reconstructed one minimum-length tree using Wagner parsimony, which was rooted with restriction site data from species of sect. *Phaeostoma* (*C. xantiana*) and sect. *Rhodanthos* (*C. amoena*). Percentages below branches are bootstrap values. Note the position of *C. (=Heterogaura) heterandra* (arrow).

fruit evolution in *Clarkia* that may be approached experimentally (e.g., how and why did the nut-like fruit of *C. heterandra* originate from the typical capsular fruit of *Clarkia*?). Discovery of the unexpected relationship of *C. heterandra* to other species of *Clarkia* offers a new avenue for expanded biosystematic and evolutionary research in the genus.

Another Californian example of phylogenetics serving to guide biosystematics is from the research of Baldwin and colleagues on the origin of the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*; Compositae). Carlquist (1959) demonstrated unequivocally on the basis of anatomical comparisons that the Hawaiian-endemic silversword alliance was most closely related to *Madieinae*, a primarily Californian group known as tarweeds or tarplants. Subsequent attempts to seek biosystematic evidence about the precise relationship of the Hawaiian species to the California tarplants was stymied by the inability to produce hybrids between members of the two groups (G. D. Carr and D. W. Kyhos personal communication). A chloroplast DNA phylogeny of the Californian and Hawaiian species refocused this biosystematic effort by suggesting that species of *Madia* and *Raillardopsis* are the closest living relatives of the Hawaiian silversword alliance (Baldwin 1989; Baldwin et al. 1991), a result corroborated by later phylogenetic analysis of nuclear ribosomal DNA sequences (Baldwin 1992; Fig. 2). In ad-

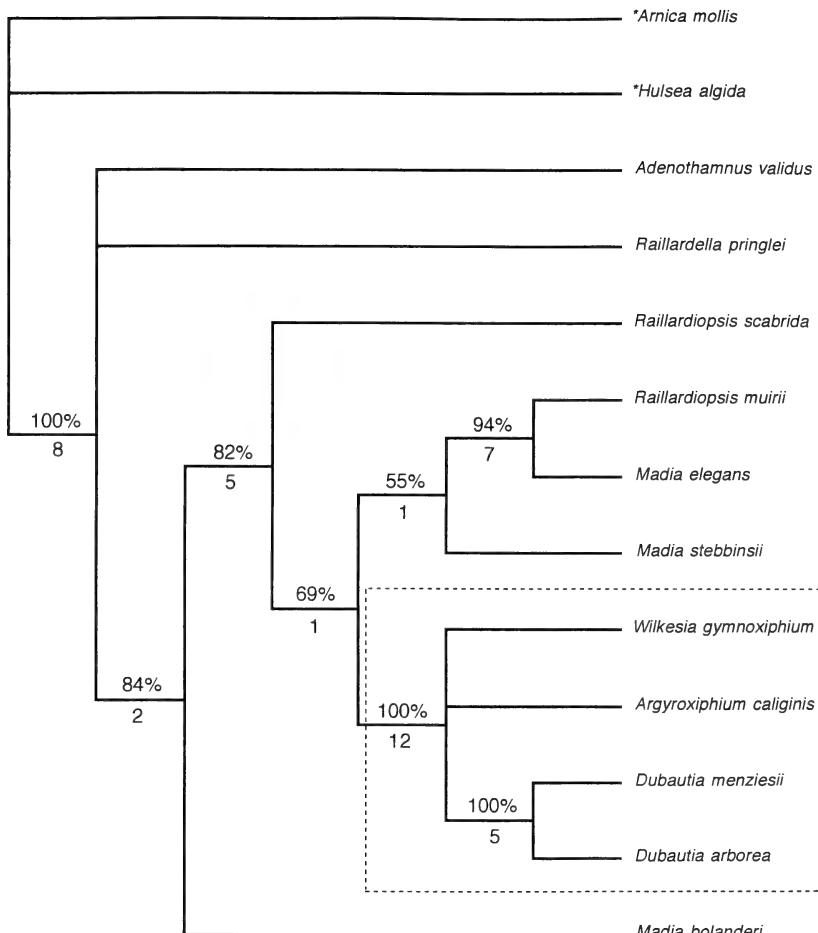


FIG. 2. Phylogenetic tree of select species from Californian and Hawaiian Madiinae (Compositae) based on internal transcribed spacer sequences of nuclear ribosomal DNA (modified from Baldwin 1992). This phylogeny is the strict consensus of the six minimum-length trees reconstructed using Fitch parsimony. Asterisks denote outgroup species. Percentages above branches are bootstrap values. Numbers below branches are decay index values. Dashed box surrounds the lineage of Hawaiian silversword alliance species. Note that the Hawaiian lineage is derived from within a grade of California tarplant species in *Madia* and *Raillardiopsis*. A similar pattern was reconstructed by Wagner parsimony analysis of chloroplast DNA restriction site mutations (Baldwin 1989; Baldwin et al. 1991).

dition, the DNA data demonstrated that *Raillardiopsis muirii* and *R. scabrida*, previously included within *Raillardella*, are most closely related to *Madia* and the Hawaiian silversword alliance. New attempts to create hybrids between the Californian and Hawaiian groups and between *Madia* and *Raillardiopsis*, guided by knowledge

of phylogenetic relationships, were successful (Baldwin 1989; Kyhos et al. 1990; Baldwin et al. 1991).

Recognition that the Hawaiian silversword alliance originated from within a sublineage of Californian Madiinae highlights the need for Californian botanists to keep a broad geographic perspective about possible relationships of even the most narrowly endemic plants in California. Another example that reinforces this caution is from work by Crawford and colleagues on *Coreopsis* (Compositae). Well-supported phylogenetic relationships of chloroplast DNA in *Coreopsis* (Compositae) suggest that the Californian annual species, previously considered to comprise a single lineage, may not be a natural (i.e., monophyletic or even paraphyletic) group (Crawford et al. 1991). Instead, the chloroplast DNA tree suggests that five of these six annuals are more closely related to the mainland Mexican perennials, *C. cyclocarpa* and *C. mutica*, and the Californian maritime perennials, *C. gigantea* and *C. maritima*, than to the remaining Californian annual, *C. stillmanii*. Relationships among these species are the subjects of continuing investigation by Crawford.

Despite the widespread perception that phylogenetics cannot be applied to groups with a history of hybridization, phylogenetic analysis can, in fact, serve to test biosystematic hypotheses of introgression or reticulation, in part by taking advantage of the different modes of inheritance of nuclear and organellar genes. The genus *Helianthus* (Compositae) provides an important example of this type from the California flora. Rieseberg et al. (1988) used phylogenetic analysis to reanalyze reported introgression between *H. annuus* and *H. bolanderi* in northern California. According to the classic hypothesis of Heiser (1949), introgression of genetic material from *Helianthus annuus* into the serpentine race of *H. bolanderi* ("exilis") gave rise to the ruderal form of *H. bolanderi* ("weedy"). If this hypothesis is true, ruderal *H. bolanderi* should possess a subset of the biparentally-inherited nuclear markers of both parents and one of the uniparentally-inherited chloroplast DNA genomes of the parents. In fact, Rieseberg et al. (1988; Fig. 3) found that ruderal *H. bolanderi* possessed four unique chloroplast DNA and nuclear DNA markers that were not found in either of the presumed parental species. Phylogenetic analysis showed that these markers were best interpreted as mutations that had arisen following divergence of ruderal *H. bolanderi* from a common ancestor with serpentine *H. bolanderi*. Furthermore, all sampled individuals of serpentine *H. bolanderi* and *H. annuus* possessed chloroplast DNA markers that were absent in ruderal *H. bolanderi* and had apparently arisen since these entities shared a common ancestor with ruderal *H. bolanderi*. These data demonstrated that ruderal *H. bolanderi* is the sole representative of an ancient lineage rather than a recent product of introgressive hybridization.

Phylogenetic studies have also helped to advance our understand-

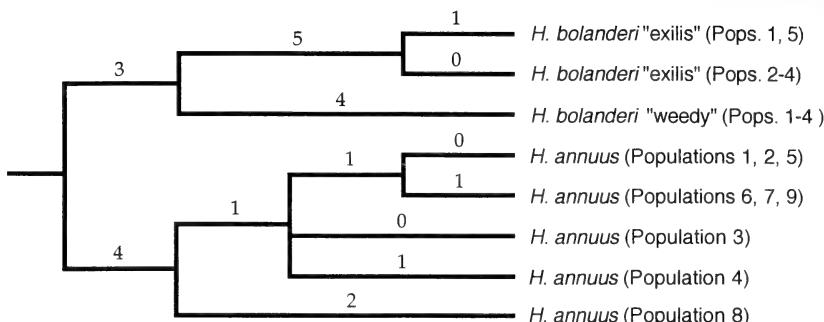


FIG. 3. Phylogenetic tree of 18 populations of *Helianthus annuus* and *H. bolanderi* (Compositae) based on chloroplast DNA and nuclear ribosomal DNA restriction site mutations (redrawn from Rieseberg et al., 1988). Rieseberg et al. reconstructed one minimum-length tree using Wagner parsimony, which was rooted with restriction site data from *H. maximiliani*. Numbers of restriction site mutations appear above branches. Note the four restriction site mutations that distinguish *H. bolanderi* "weedy" from *H. annuus* and *H. bolanderi* "exilis".

ing from biosystematics of the origin of hybrid and polyploid species in California. In *Microseris* (Compositae), Jansen and coworkers reexamined the origins of the Californian allotetraploids *M. decipiens* and *M. heterocarpa* from the perspective of a chloroplast DNA phylogeny and nuclear ribosomal DNA markers. They found that *M. (Uropappus) lindleyi*, suggested by biosystematic results to be one parent of the allotetraploids (see Stebbins et al., 1953; Chambers 1955), was actually more closely related to all members of *Agoseris* and *Nothocalais* than to *Microseris* sensu stricto, which includes the other putative, maternal parents of *M. decipiens* and *M. heterocarpa* (Jansen et al. 1991). These findings indicated that the hybridization events involved in the origins of the allotetraploids were between more distantly related species than had been appreciated previously. In *Raillardella* (Compositae), a genus of three primarily Californian, montane tarplant species, origin of the polyploid *R. scaposa* ($n = 34, 35$) was unclear from cytological analysis of synthetic hybrids with *R. pringlei* ($n = 17$), which possesses the same genomic arrangement as *R. argentea* ($n = 17$) (Baldwin 1989; see Kyhos et al. 1990). Subsequent phylogenetic analysis of nuclear ribosomal DNA sequences from the three species indicates that *R. scaposa* is an allopolyploid involving species similar or identical to *R. argentea* and *R. pringlei*.

Phylogenetic studies can also help to distinguish among polyploid entities that have arisen independently but are morphologically and chromosomally similar. In *Microseris*, the chloroplast DNA tree of Wallace and Jansen (1990) provided evidence that "*M. heterocarpa*"

may be a polyphyletic species that includes populations that arose from at least two independent hybridization events between *M. lindleyi* and different annual taxa in *Microseris* (possibly different subspecies of *M. douglasii*). This observation, of course, calls into question the naturalness of this apparently polyphyletic species. In *Heuchera* (Saxifragaceae), Soltis et al. (1989) provided phylogenetic evidence from chloroplast DNA that indicates multiple origins of autoploidy within *H. micrantha*, a species that includes diploid and polyploid populations, in northern California and the Pacific Northwest. Three origins of autoploidy were inferred within one variety (*H. m.* var. *diversifolia*) alone.

Our understanding of diploid chromosome evolution in the California flora can also benefit from a phylogenetic perspective. Such cytogenetic clarification was obtained in *Calycadenia* (Compositae), a Californian genus of tarplants in which extreme chromosomal repatterning has occurred. Elegant cytological work on these species by G. D. Carr and R. L. Carr resolved cytological relationships in much of *Calycadenia* (see Carr 1975a, b; Carr and Carr 1983). Extensive chromosomal structural divergence of some species and lack of chromosomal association at meiosis in some hybrids, however, prevented comprehensive cytogenetic analysis (see Carr 1977). A highly-resolved and well-supported phylogeny of *Calycadenia*, based on nuclear ribosomal DNA sequences, extends understanding of evolution in chromosome numbers and chromosomal arrangements within the genus (Baldwin 1993; Fig. 4).

Baldwin's ribosomal DNA tree (Fig. 4) indicates that the only species of *Calycadenia* with a chromosome number of $n=9$, an absence of tack-glands, and an extreme southern California distribution, *C. tenella*, can be justifiably treated as a monotypic genus, *Osmadenia* (because *O. tenella* is the sister group of *Calycadenia*), in corroboration of Carr's (1975a) conclusions. The ribosomal DNA tree also supports Carr's hypothesis (1975a) that chromosome number differences in *Calycadenia* sensu stricto arose by descending dysploidy from a base number of $n=7$. The phylogeny extends the cytogenetic perspective by showing that two independent dysploid reductions in chromosome number from $n=7$ occurred in genus: one that gave rise to all species with $n=6$ and 5, and another that resulted in the only species with $n=4$, *C. spicata*. Further, the phylogenetic relationship of *C. hooveri* and *C. villosa* and their near-identity in chromosome arrangement (Carr 1975b) offers an insight into the actual chromosome arrangement possessed by the immediate ancestor of both sister dysploid lineages. Based on the combined perspective of these chromosomal and phylogenetic data, the ancestor of all species with $n=4$, 5, or 6 possessed a $n=7$ genome similar or identical in structure to that of either *C. hooveri* or *C. villosa*. Recognition that *C. hooveri* and *C. villosa* preserve (near-)

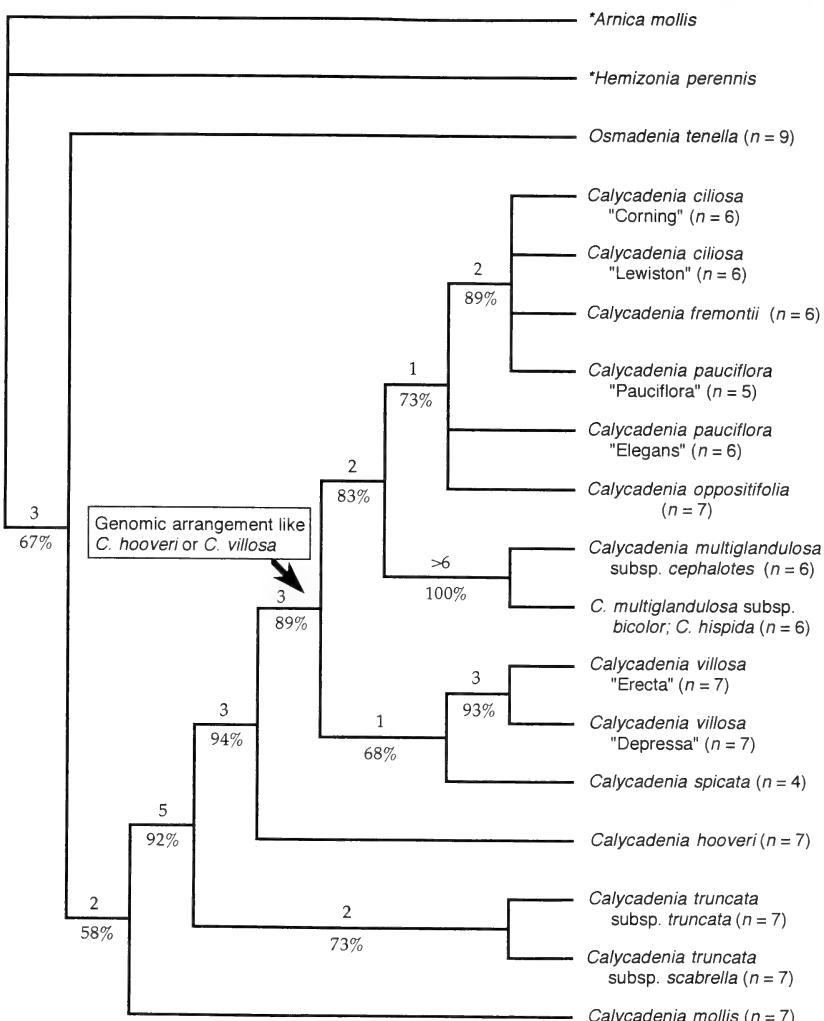


FIG. 4. Phylogenetic tree of *Calycadenia* (Compositae) based on internal transcribed spacer sequences of nuclear ribosomal DNA (modified from Baldwin 1993). This phylogeny is the strict consensus of the 11 maximally parsimonious trees reconstructed using Fitch parsimony. Asterisks denote outgroup species. Bootstrap values appear below branches. Numbers above branches are decay index values. Haplloid chromosome numbers follow species names. Note the phylogenetic positions of *C. hooveri* and *C. villosa*, which share similar chromosome arrangements (Carr 1975b), and the consequent implication for the ancestral genome of both dysploid lineages (arrow).

relict chromosomal arrangements that may be of pivotal importance to understanding chromosome evolution in *Calycadenia* increases the conservation priority of these two rare species (both on CNPS List 1B, Skinner and Pavlik 1994).

Prominent examples of speciation modes from the California flora, based largely on biosystematic data, can also be tested and further refined with phylogenetic information. For example, phylogenetic analysis of *Layia* (Compositae) has offered a new outlook on the classic geographic speciation model proposed for this genus by Clausen, Keck, and Hiesey (see Clausen 1951), elaborated upon by Stebbins (1966), and further studied by Warwick and Gottlieb (1985). Clausen (1951) showed that in *Layia* highly interfertile species are allopatric, or effectively so, whereas truly sympatric species are of low interfertility or are apparently cross-incompatible. From these considerations (and secondary morphological criteria), it was concluded that speciation in *Layia* occurred during periods of geographic separation between gradually diverging populations, with sympatry arising after the development of reproductive barriers. This conclusion was based on the assumption that levels of fertility and chromosomal association at meiosis in hybrids were indicative of recency of common ancestry of the parental species. This presupposition violates the concept that derived characteristics diagnose relationships and further assumes that species interfertility and chromosomal homology (as reflected by extent of meiotic chromosomal association) decay gradually at similar rates throughout lineages. Violation of these assumptions in *Layia* could significantly alter inferred species relationships and, in turn, reduce conformity with the geographic speciation model.

Preliminary phylogenetic results from studies of nuclear ribosomal DNA sequences (Baldwin 1994, in prep.) suggest that species relationships are largely in accord with Clausen's assumptions: species that are highly interfertile and allopatric (e.g., *L. jonesii* and *L. munzii*) indeed appear to share a more recent common ancestry than species that are widely sympatric and of low interfertility (e.g., *L. chrysanthemoides* and *L. platyglossa*). In addition, extensive ribosomal DNA sequence divergence between species parallels high genetic divergence between species in allozymes (Warwick and Gottlieb 1985), thereby reinforcing Warwick and Gottlieb's (1985) conclusion that genetic evidence is consistent with gradual divergence of *Layia* species. Clausen's assumptions do appear to be violated by *L. carnosa*, however, which appears to be most closely related to species with which it is reportedly either intersterile or cross-incompatible, *L. gaillardioides* and *L. hieracioides*. In contrast, *L. pentachaeta* is partially interfertile with *L. gaillardioides* and *L. hieracioides*, but apparently more distantly related to these taxa than is *L. carnosa*. These unanticipated relationships, suggested by the ribo-

somal DNA phylogeny, are also among the best supported results from phylogenetic analysis of Clausen's morphological data matrix of *Layia* (Clausen 1951; Baldwin, in prep.).

The foregoing examples illustrate a few of the potential uses of phylogenetic information in conjunction with biosystematic data to advance our understanding of California plant diversity and diversification. From a practical standpoint, the importance of such evidence for taxonomy, floristics, and conservation efforts cannot be overemphasized. Realistically, we rely on taxonomy to reflect the natural lineages of life that are recognized as worthy of concern and protection. In turn, taxonomy must rely on phylogenetics and other systematic research to discern those critical lineages. In addition, floristic studies depend on a natural taxonomy for accurate estimates of biodiversity and as a basis for meaningful comparisons within and between bioregions. The California flora is sufficiently complicated and endangered to demand such detailed study in order to wisely set conservation priorities and to insure that limited conservation resources are used judiciously.

Biosystematic and phylogenetic studies are important components of the education and research program in plant systematics, conservation, and floristics at the Jepson Herbarium. The ability of the Jepson Herbarium to promote all types of California botanical studies, including biosystematic and phylogenetic investigations, has been greatly enhanced by the generosity of the previous Curator, the late Dr. Lawrence R. Heckard. Dr. Heckard's influence will continue to be felt at the Jepson Herbarium in many ways, including the Heckard Fund, established by Larry for continued research on the California flora into posterity.

ACKNOWLEDGMENTS

I thank Brent D. Mishler, John L. Strother, and an anonymous reviewer for helpful comments on the manuscript.

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(Received 28 Oct 1994; accepted 3 Feb 1995)

THE THREAT TO THE CALIFORNIA FLORA FROM INVASIVE SPECIES; PROBLEMS AND POSSIBLE SOLUTIONS

KRISTINA A. SCHIERENBECK
California State University, Fresno,
Department of Biology, Fresno, California 93740

ABSTRACT

Non-native invasive plant species continue to threaten the persistence of native plant species and communities in California. Progress toward the control of non-native invasive species can only be made through the combined consideration of ecological and political solutions. These solutions require greater cooperative effort between the academic and lay botanical communities toward understanding the specific impacts and habitat requirements of invaders on a per species basis. Only thorough ecological understanding will lead to the effective implementation of habitat management plans that discourage invaders and encourage the proliferation of native species. Although these recommendations are long-standing, applied and theoretical research on invasive plant species, their habitat requirements and ecological impacts, remains low. Until more data can be gathered and disseminated, the interim solution of local invasive species removal is essential in controlling nascent and potentially aggressive populations. Effective control measures must be combined with the continued education of governmental agencies, horticultural organizations, lobbying groups, and the gardening public regarding the importance of discouraging the use of invasive exotic species for horticultural or land management purposes.

The deterioration of geographic and biological obstacles to the global dispersal of species and human-caused disturbance have dramatically increased in this century and with these changes, plant communities have become more susceptible to invasion from non-indigenous species (Elton 1958, D'Antonio and Vitousek 1992). Although the threat of non-indigenous species to the integrity of native plant communities and species diversity has been recognized for decades (Baker 1962, Dasmann 1966), the urgency of the problem has finally become apparent (Huenneke 1988, Temple 1990). As disturbance to natural ecosystems becomes a more widespread phenomenon, a clearer understanding of the biology and ecological relationships of invasive species is critically important to the conservation of native plant communities.

In California, population growth and its associated commerce and agriculture have led and continue to lead to the introduction and establishment of invasive non-native species since the mid-18th century (Mooney and Drake 1987). These factors disrupt native ecosystems through the direct removal or degradation of native vegetation and result in both the intentional and unintentional intro-

duction of new species (Kruger et al. 1989). The moderate climate throughout much of California, combined with the early and continued importation of garden ornamentals contribute to the foray of exotic species (Mack 1991). Traits favored for hardy garden ornamentals are often traits repeatedly suggested as important to successful invaders; these traits include continual sexual reproduction, rapid establishment, and hardy growth under a variety of climatic and edaphic conditions (Baker 1974). Rapidly growing and reproducing species often favored for the stabilization of landscapes following fire and landslides have resulted in some of California's worst invaders; these include *Cortaderia jubata*, *Carpobrotus edulis*, *Ammophila arenaria* and *Lolium multiflorum*.

The potential impacts from invaders on the native flora and plant communities include genetic contamination (Ellstrand 1992), the reduction of species diversity, alterations to successional patterns (MacDonald et al. 1988), and changes to the physical characteristics of ecosystems and ecosystem processes (Vitousek 1986). Hybridization and introgression between native species and their invasive congeners has been substantiated in species of *Helianthus* (Rieseberg et al. 1989) and with one of the rarest tree species in California, *Cercocarpus traskiae* (Rieseberg et al. 1989). There is, however, little information on the extent of hybridization between native and introduced species and its possible consequences at the community or ecosystem level (Ellstrand 1992). Although it is debatable whether *Carpobrotus chilensis* is native to California or to Chile (Bicknell and Mackey 1988, Vivrette 1993), its hybridization and introgression with the aggressive South African native, *C. edulis*, is one of the most widespread examples of hybridization between previously allopatric species. Current research is exploring the potentially important genetic and ecological implications of this hybridization (D'Antonio and Schierenbeck unpublished data).

Establishment of an invader in a community can result in the loss of species diversity and the alteration of successional patterns (MacDonald et al. 1988). Although much anecdotal evidence exists in California (see *Fremontia* vol. 12, no. 4 and vol. 13, no. 5), little is known about which native species are most susceptible to encroachment from an invasive species or the measurable extent of change an invader can bring to a plant community.

It has been well-established that invaders can bring change to the physical characteristics of ecosystems (Vitousek 1986, D'Antonio and Vitousek 1992). This phenomenon has been documented with *Myrica faya*, which can alter nutrient cycling (Vitousek et al. 1987), *Tamarix* spp. which can alter hydrological regimes (Brotherson and Field 1987, Loope et al. 1988) and with grasses such as *Schizachyrium condensatum* which can modify the frequency of fire-cycles (Hughes et al. 1991). Despite the number of invaders in California

that are suspected of possessing the ability to alter the physical characteristics of ecosystems, there are few such long-term ecosystem studies.

The obstacles which need to be overcome in making progress in the battle against invasive species are many but include some particularly important aspects. First and foremost, there needs to be stronger recognition of and action taken against the causes of invasive species proliferation. Disturbance is recognized as a major source of entry for invasive species, yet it continues in many forms. Secondly, there is a need for more empirical studies on the biology and ecological interactions of invasive species and the data resulting from such studies need to be more effectively applied to the management of conservation areas. Lastly, increased funding for the eradication of new and old populations of invasive species combined with improved detection and reporting methods of new occurrences will aid in their containment. These hinderances to the understanding and control of invasive species are described in more detail below.

Probably the most significant factor in the continual proliferation of invasive species is the physical disruption of plant communities and alterations to their disturbance cycles (Orians 1986, Hobbs and Huenneke 1992). Disturbance comes in many forms, virtually all of which offer a potential point of entry for invasive species. Examples of types of disturbance include: the disruption of natural disturbance regimes through grazing or fire suppression which can favor non-native species preadapted to the altered condition (Hobbs and Huenneke 1992); the gradual establishment and encroachment of an invasive species which can itself result in the perpetuation of an altered disturbance cycle (Hughes et al. 1991); small conservation areas which, by definition, have large edges and thus large zones of disturbance; and conflict between conservation and recreation within or near a natural area which can maintain low-level disturbance and the continual import of invaders. Considering the plethora of examples of both disturbance and the occurrence of non-native species in California, there have been surprisingly few empirical studies on these phenomena as they relate to ecological interactions within native plant communities.

Often the assumption is made that if an area is preserved it will be maintained in a natural state. However, it has become clear that wilderness or conservation areas, with the exception of those in places like Alaska, are not sufficiently large to maintain the large or even small scale disturbances necessary to maintain community diversity at a level that existed prior to the human perturbation (Brussard 1991). Discerning the ecological relationships between an invader, the community in which it occurs, and disturbance can often require subtle detective work. For example, recent work with

disturbance and pollinator populations in Argentina suggests small conservation areas support primarily those species that accept the most generalist pollinators (a trait common in invaders) (Aizen and Feinsinger 1994). The selection of generalist pollinators in small conservation areas can result in a larger seed set for the invaders and may reduce genetic diversity in those species with more specific pollination systems. The secondary and even tertiary impacts of disturbance and their role in non-native species proliferation needs to be discerned empirically.

Since the first seminal meeting on colonizing species in which the characteristics of invaders were outlined (Baker and Stebbins 1965), there have been attempts to make predictions as to which species have the greatest potential to become invasive (Bazzaz 1986, Newsome and Noble 1986). Recent research suggests the invasiveness of a species is not due to the general traits of the invader per se but to the fit of a species' characteristics with specific habitat characteristics (Bossard 1993, Schierenbeck et al. 1994). Not until there is a thorough understanding of how each invader functions in its new range environment will there be some modicum of control against these pests. The recent finding that *Cytisus scoparius* has differential germination in coastal and Sierra Nevadan habitats provides information that can be used toward its control through prescribed burning (Bossard 1993). Bossard's study underscores the need for understanding the specificity of the relationship between invaders and their new range habitat.

Funding for conservation efforts has often centered on the preservation and recovery of rare species. Unfortunately, the conservation of rare species and plant communities cannot be achieved without a better understanding of threats to the survival of the ecosystems in which they occur. In some cases, large amounts of funds and effort have been expended toward removing invasive species in conservation areas as illustrated by attempts to eradicate *Ammophila arenaria* (Van Hook 1985). However, it is difficult to maintain progress against these control efforts without understanding what factors allow an invader to proliferate. Subtle relationships can exist between a species' phenology, response or lack of response to herbivory, and disturbance (Schierenbeck et al. 1994). Where the factors encouraging the expansion of invasive species are unknown, management regimes could inadvertently encourage growth, reproduction and dispersal.

Regional, state and federal parks are under heavy impact from recreational and agricultural use. Although conservation areas are set aside for protection, they are often too small or heavily used to maintain ecosystems in a natural state without heavy management input. Those natural areas in close proximity to urban centers are particularly susceptible to disturbance and to the dispersal of non-

native species. Unfortunately, land use conflict within and around natural areas is a problem without easy resolution. Lands managed by the U.S. Forest Service have recently been issued a respite in the battle against invasive species. The U.S.F.S. has issued a policy on the management of noxious weeds and their control and hopefully will follow through with its strong implementation. The California Department of Food and Agriculture continues to provide leadership in controlling invasive species, however their emphasis remains on those species that have primary impacts on agricultural lands.

The deliberate and continued reintroduction of invasive species is a practice which defies comprehension but continues for political expediency. For example, *Lolium multiflorum* is still being used for reseeding efforts under the auspices of governmental action even though its short- and long-term benefits are questionable (Zedler et al. 1983, Barro and Conard 1987).

It is becoming increasingly obvious that the maintenance of natural ecosystems can require intensive management (Brussard 1991). In summary, obstacles to the effective management of ecosystems in a state that existed prior to European influence are: an under-funding of biological and ecological studies of invasive species and the communities that they invade, a lack of adequate fund sources for the detection and eradication of invasive species in non-agricultural systems, a lack of strong agency policy toward resolving conflicts that influence the effectiveness of control efforts, continued reintroductions of invasive non-native species, and continued and new disturbances.

Where do we go from here? Policy decisions for habitat management must be based on sound data, however, in most cases this is not possible and the problems are immediate. Much of existing knowledge of invasive species exists in the form of anecdotal information in the lay botanical community. Although it in no way diminishes the need for scientific experimentation, the dissemination of anecdotal information on the occurrence and effective control of invasive species needs to be improved. The continued detection and eradication of growing populations of invaders is crucial to their control. Detection efforts could be enhanced through the increased use of geographic information systems as has been successfully demonstrated with the *Centaurea solstitialis* (Parris and Pitcairn unpublished data). Removal efforts should be prioritized based on those species which have been determined to result in the greatest amount of change to community or ecosystem characteristics. The continued education efforts of the California Native Plant Society and the California Exotic Pest Plant Council are vital to informing the lay public of the potential threats from non-indigenous species and as conduits of information to and from the scientific community.

Steps toward lessening the invasive species problem in the man-

aged ecosystems of California are led by the need to gain a clearer understanding of the specifics of each invasive species' biology and ecological interactions within a specific ecosystem, and the relative role of disturbance in the ecosystem of interest. Introduced species must be studied in their host ecosystem; synergistic relationships with native constituents can only be determined empirically. Habitat management plans need to be based on long-term experimentation. Just how are successional relationships and species diversity within a particular community affected by disturbance and invasive species? The opportunities of entry and proliferation for invasive species need to be identified on a case-by-case basis. Is the proliferation of an invasive species due primarily to disturbance or to the combined effects of competition, disturbance and the disruption of ecosystem characteristics? The control of invasive species includes an increased need for the widespread acceptance and implementation of the intensive management of ecosystems. It is unrealistic to expect an ecosystem to remain self-perpetuating with the small sizes and continual disturbances with which we are faced.

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(Received 9 Sep 1994; accepted 20 Jan 1995)

FUTURE OF CALIFORNIA FLORISTICS AND SYSTEMATICS: WILDFIRE THREATS TO THE CALIFORNIA FLORA

JON E. KEELEY

Department of Biology, Occidental College,
Los Angeles, CA 90041

ABSTRACT

The primary threat to the California flora posed by wildfires is through human intervention with the natural fire cycle. Fires at frequent intervals, e.g., less than 5 years, can have devastating impacts on the survival of fire-adapted species. Aerial seeding of burned habitats poses another significant threat, as seeded species are capable of competitively displacing natives as well as creating conditions conducive to repeat fires.

Much of the California flora is adapted to disturbance by wildfires and indeed species in some communities, such as chaparral and coastal sage scrub, have been described as "fire-dependent". Today, fires typically occur at intervals of 20–50 years, but there is some controversy as to what the natural fire frequency was (Keeley et al. 1989). Resilience of the flora to deviations from the contemporary fire regime is highly dependent upon the direction of the deviation; i.e., fires at less frequent intervals result in quite different community responses than fires at higher frequencies.

Theoretically, anthropogenic fire suppression, resulting in longer than natural fire-free durations, could have negative impacts on fire-dependent species, although, due to a largely unsuccessful fire-prevention program, few areas escape fire for unusually long periods. Studies of remnant stands of century old chaparral have not revealed evidence that even this extreme length of fire-free conditions poses a threat to the persistence of any species (Hedrick 1951, Keeley 1992). Additionally, century old stands appear to recover normally from fire (Keeley and Zedler 1978), although this has not been studied in great detail.

A far greater threat to the California flora are deviations on the short end of the fire return interval. In chaparral and coastal sage scrub, fires at frequencies of every few years are largely anthropogenic in origin. Humans provide a ready source of ignition during the driest time of the year and often coinciding with extreme Santa Ana conditions. In addition, humans create conditions conducive to wildfires through so-called postfire rehabilitation projects. Aerial seeding of burns with ryegrass and other non-native species creates

an ideal fuel bed for recurrent fires; these species typically dry out sooner in the spring than natives and form a more continuous plant cover, which more readily carries a fire. Zedler et al. (1983) showed how a seeded chaparral site was exposed to a second reburn after one year and this resulted in the extirpation of *Ceanothus* from the site. Recent studies have also shown how frequent fires can replace the native flora with non-native grasses and forbs (Fig. 1). Even so-called fire-annuals, specifically adapted to postfire conditions, can not persist under repeated fires, as they are poorly equipped to compete with the non-native weeds.

Multiple fires during periods of five to 10 years have been implicated in the type conversion of chaparral and coastal sage scrub to non-native annual grasslands (Keeley 1990). Even longer intervals may be threats for some species. For example, *Cupressus forbesii* Jepson (Tecate cypress) has been shown by Zedler (1977) to be reduced by fires at 30-year intervals and greatly threatened by fires at 10-year intervals.

An additional threat of postfire seeding is the potential competitive displacement of the native flora. An example of a couple such sites that have received this sort of postfire treatment over many decades are shown in Table 1. The Kinneloa (or Altadena) Fire burned in the foothills of the San Gabriel Mountains above Altadena, California in autumn 1993. In addition to the native flora having to compete with the dense growth of ryegrass *Lolium multiflorum* Lam. (ryegrass) and zorro fescue *Vulpia myuros* L. C. Gmelin (zorro fescue) seeded by the U.S. Forest Service, they are also being choked by a dense stand of other non-natives, largely the mustard *Hirschfeldia incana* (L.) Lagr.-Fossat (formerly *Brassica geniculata* [Desf.] Ball). The dominance of this species possibly reflects the "ghost of seedings-past", as mustards were the species of choice for postfire rehabilitation projects beginning in the 1930's and lasting several decades, particularly in the San Gabriel Mountain foothills (Went et al. 1952, Barro and Conard 1991). The persistence of these mustards is in part due to their polymorphic seed bank, a portion of which is dormant and fire-stimulated (Keeley et al. 1985). On the bright side, botanists should be thankful that 40 years ago resource managers recognized the invasiveness of mustard species and halted their use in postfire rehabilitation projects.

Increasingly resource managers are recognizing the negative impacts of postfire seeding and are proposing alternative approaches to management of burned habitats. One approach considered more environmentally-sound is the use of native species in postfire seeding of burns. However, two potential threats to these communities are:

1. The ecological consequences of broadcasting natives into situations where their natural occurrence may be low. For example, many species are quite restricted in their natural distribution, such

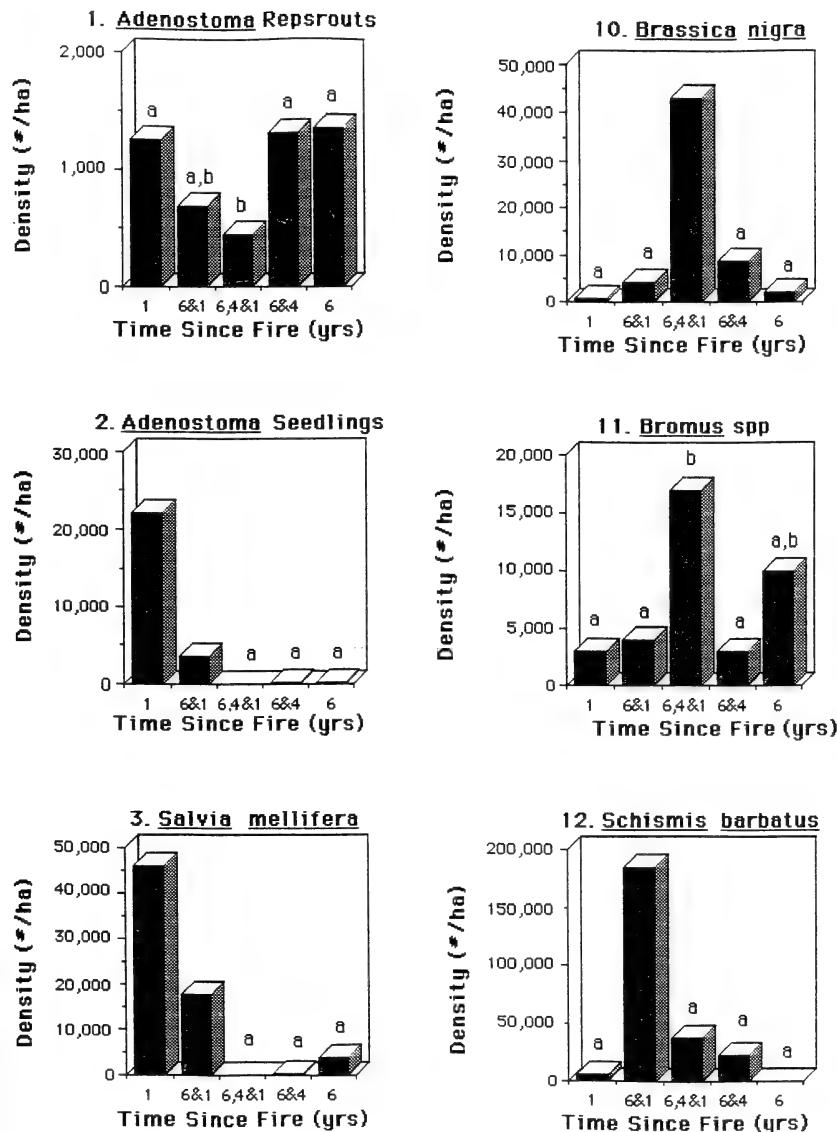


FIG. 1. Density of dominant shrubs (left) and non-native herbs (right) in adjacent chaparral sites subjected to different fire frequencies (horizontal labels, left to right are: site burned 1-year prior to study, 1 & 3 years prior, 1, 4, & 6 years prior, 4 & 6 years prior and 6 years prior; bars capped with same letter are not significantly different at $P > 0.05$ with 1-way ANOVA). Data from Haidinger and Keeley (1993).

TABLE 1. PLANT COVER ON TWO SITES WITHIN THE SEEDED PORTION OF THE 27 OCTOBER 1993 KINNELOA FIRE. Sites were aerially seeded with *Vulpia myuros*, *Trifolium hirtum*, *Lolium multiflorum*, *Lotus scoparius*, and *Eschscholzia californica* 16–18 November 1993 and sampled 7–28 March 1994. Data from Keeley unpublished.
a Native species seeded on the site were indistinguishable from those same species arising from indigenous seed; all are included under “seeded species”.

Site	Coverage (cm ² plant cover/m ² ground surface)					
	Seeded species ^a		Natural regeneration			
	Native	Non-native	Perennial herbs	Annuals	Shrubs	Non-natives
Eaton Cyn	200	826	610	716	547	8313
Lake Ave	442	4860	21	913	162	5514

as only on south-facing slopes. Their introduction onto north-facing slopes by seeding may result in undesirable competitive interactions with the north slope plant species.

2. The genetic effects of seeding must be considered, as introduction of non-local seeds may swamp local genotypes, or outbreeding depression may reduce seed set or the vigor of the subsequent generations.

CONCLUSION

Human intervention in the natural fire cycle poses a significant threat to some components of the California flora.

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(Received 7 Oct 1994; accepted 10 Feb 1995)

THREATS TO THE CALIFORNIA FLORA: UNGULATE GRAZERS AND BROWSERS

ELIZABETH L. PAINTER

Jepson and University Herbaria,
University of California, Berkeley, CA 94720

ABSTRACT

While herbivory probably is a natural part of all terrestrial ecosystems, livestock herbivory is not a natural part of California's natural ecosystems. In California, mammalian herbivores can range in size from small rodents to large ungulates. However, the potential of threats is greater from ungulates, which include native taxa (e.g., tule, Roosevelt, and Rocky Mountain elk, mule deer, pronghorn antelope) and alien livestock (e.g., cattle, horses, burros, sheep, goats). Impacts of the native ungulates are not well studied. There are few, if any, types of plant communities in California that are unimpacted by livestock. Livestock herbivory is a threat to some rare plant taxa. Livestock impacts can include alterations in species composition of plant communities, in ecosystem function, and in ecosystem structure. Although the impacts can be severe, in terms of negative impacts on native plants, carefully managed livestock herbivory may not be the most destructive land use practice.

Herbivory is a natural part of most (if not all) ecosystems. However, not all herbivory is equivalent and activities of different species of herbivores produce very different effects. Few people would expect the effects of grazing activities of grasshoppers and bison to be similar, but it is less obvious that even two superficially similar grass specialists, such as bison and cattle, use the landscape differently, feed on different plant species, have different digestive efficiencies, etc. There are no simple substitutions among taxa.

In California, mammalian herbivores can range in size from small rodents to large ungulates. Although small mammals do impact and sometimes significantly alter their environment (e.g., Cox 1984, 1986, 1990, Hobbs and Hobbs 1987, Hobbs and Mooney 1985, Koide and Mooney 1987), the potential of threats is greater from larger animals.

There is limited consensus as to the effects of ungulate herbivory. There is not even agreement on definitions of terms. As one scans the "grazing" literature, one finds "to graze" is used to mean (1) any type of consumption of aboveground production of both woody and herbaceous plants (not just fruits or seeds), (2) to feed primarily on herbaceous plants, or (3) to feed primarily on grasses or graminoids (Poaceae, Cyperaceae, Juncaceae). "To browse" is used to mean to feed primarily on (1) woody plants or (2) nongrasses or nongraminoids. A statement such as "grazing is a natural process on all plant

communities" (Box and Malechek 1987) takes on different meanings, depending upon the definition used. Both "browse" and "graze" may be used only for defoliation or may include some or all ancillary impacts (e.g., trampling, excrement, pull-up and breakage). In this paper, I am using definition 2 of "graze" (to feed primarily on herbaceous plants), definition 1 of 'browse' (to feed primarily on woody plants), and 'herbivory' for a combination of the two. I am including ancillary impacts with all three terms. These categories are generalizations; "animals are neither plant taxonomists nor community ecologists and consume plants according to [plant] availability and [the animal's] preference" (Huston and Pinchak 1991).

Large ungulates in California include native taxa (e.g., tule, Roosevelt, and Rocky Mountain elk, mule deer, pronghorn antelope) and aliens (e.g., cattle, horses, burros, sheep, goats)—a mixture of grazers, browsers, and facultative browser/grazers. The native ungulates are facultative browser/grazers or browsers, rather than grazing specialists like cattle (Murie 1951, Vallentine 1990).

There have never been modern plains bison (a grazer) in what is now California (McDonald 1981, D. Van Vuren, personal communication). The extinct prehistoric bison were quite different in morphology, habitat preference, and probably in herding behavior, since (like the modern European bison and the Canadian wood bison) they were browsers or browser/grazers, and probably did not congregate in large herds (McDonald 1981).

Before European settlement, there were three elk taxa (tule, Roosevelt, Rocky Mountain), with different ranges and habitat preferences, although their ranges apparently did overlap slightly in northern California and there apparently was some hybridization (C. Schonwald-Cox, personal communication). Roosevelt elk lived along the north coast, in places similar to Prairie Creek Redwoods State Park. Tule elk were found in drier areas than Roosevelt elk, inhabiting much of the oak woodland and savanna, primarily in and around the Central Valley. Tule elk are not native to some areas where they live in reserves today, (e.g., Point Reyes National Seashore). Rocky Mountain elk were found only in extreme northeastern California. Elk are highly versatile and opportunistic in diet choice, utilizing a broad range of herbaceous and woody vegetation (Murie 1951, Jenkins and Starkey 1991). Grasses can be an important component. Mule deer were found in woodlands, savannas, riparian zones, and post-burn chaparral. They are seasonally facultative browser/grazers, utilizing more herbaceous plants during the growing season and more woody plants during the rest of the year (Vallentine 1990). Pronghorn were found in drier, more open habitats, including desert habitats. They are browers, and grass is only a minimal part of their diets (Vallentine 1990).

In California, there are quite a few alien ungulates, both domestic

livestock and feral animals descended from livestock. Domestic livestock include sheep, goats, horses, burros, and cattle. Occasionally they also include ungulates native to California but not to the local area (e.g., elk and deer on Santa Rosa Island). Feral ungulates include burros, horses, sheep, and goats. Management regimes designed to remove feral animals or to minimize their impacts vary with species and location, and success has also varied. Feral horses and burros are protected by law, so only live removal is permitted. Because live removal is difficult, sheep and goats are usually killed. However, killing has upset animal-rights groups and has been stopped in some areas. Burros, horses, and sheep are grazers or browser/grazers (depending on habitat), and goats are browsers or browser/grazers (Vallentine 1990). Cattle are grazers and, whenever possible, cattle feed primarily on grasses (Vallentine 1990).

In North America, the effects of native ungulates on plants in their native habitats have not been well studied, except for a few areas in the Great Plains (e.g., Wind Cave National Park, see Holland et al. 1992, Painter et al. 1993, Whicker and Detling 1988, and literature therein). There have been no such intensive studies in California.

Recently, both the scientific and popular literature have published debates about benefits and costs of alien ungulate (livestock) grazing in western North America (see Belsky 1986, 1987, Painter and Belsky 1993 for bibliography). *Fremontia* (California Native Plant Society) has published a number of articles and letters (Baker 1992, Barrett 1992, Belsky 1992, Blumler 1992, Edwards 1992a, b, 1993, Keeley 1993, Menke 1992, Stebbins 1992). There are those who strongly believe that plants and ecosystems of western North America benefit from livestock herbivory, that herbivory may be necessary to sustain the system, and that livestock are just tools (e.g., Goetz 1994, Hill 1991). Others strongly oppose these ideas (e.g., Jacobs 1991, Wuerthner 1994a, b). While there is an enormous body of literature on livestock herbivory in western North America, most of it concerns increasing livestock production or increasing forage production to feed livestock. Comparatively little research has been designed to examine what happens when livestock are removed. Nongrazed land is relatively rare, and most areas that are livestock-free are too small for valid comparisons (Bock et al. 1993). Effects of livestock may be greater west of the Rocky Mountains than on the Great Plains (Mack and Thompson 1982). Ecological costs of livestock in western North America can be dramatic (Fleischner 1994).

The impacts of livestock on plants vary, depending on animal species, numbers, and management. Both feral and domestic livestock can have significant negative impacts on plant taxa, plant communities, and ecosystems.

Individual plants can be impacted directly, by defoliation, pull-

up, breakage and trampling, or indirectly, by animal-induced changes in habitat, changes in competitive relationships among plants, destruction of seedlings, or changes in conditions so that seeds don't germinate, etc. Impacts on juveniles may be greater than on adults, greatly reducing or eliminating reproductive success. Long-lived taxa whose reproduction has been impacted by herbivores may now persist primarily through inertia (*sensu* Cole 1985). While nondefoliated plants may benefit from reduced competition from defoliated plants, there is no compelling evidence that individual plants benefit from being defoliated (Belsky 1986, Painter and Belsky 1993). Among the 1742 plant taxa listed by the California Native Plant Society as rare, threatened, or endangered, at least 225 taxa to some degree are "threatened by grazing" (Skinner and Pavlik 1994).

Livestock herbivory does not have equally negative effects on all native plants. Some plants apparently can tolerate a certain amount of herbivory; others have avoidance mechanisms. This resistance (avoidance/tolerance) to herbivory has been interpreted by some (e.g., Edwards 1992) as an adaptation to grazing. It is more probable that the resistance is a strategy to reduce the negative impacts of all types of damage (Belsky et al. 1993). Plants experience injury from a wide variety of sources besides herbivory, including fire, wind, and freezing. Plants often have similar responses to damage from several different sources. This is not the same as being 'adapted' to ungulate herbivory. Resistance to damage is not necessarily predictable. It can vary among closely related species, and even between populations of the same species (e.g., Painter et al. 1989, 1993). Some native California plant species appear to have limited tolerance of livestock grazing. However, if they are preferred foods, the resulting stress may put them at a competitive disadvantage with unpalatable plant species and with more grazing tolerant species, leading to a decline in number or even a loss from the community. However, in many areas, they appear to have been able to persist, in reduced numbers and sizes of plants, although often with little reproduction from seed. Since there is very little information available about the lifespan of these taxa, it is not known how long inertia will be enough to maintain their presence.

There are few, if any, types of plant communities in California that are unimpacted by livestock. Impacts of livestock can be found even on beaches and dunes (e.g., on Santa Rosa Island, personal observation). Intensive use by livestock (feral or domestic) has had adverse effects on many pine and cypress communities (Vogl et al. 1990). Effects of livestock on oak woodlands and savannas are equivocal (Griffin 1990). Although climate and native herbivores are often important, livestock can have a role in reducing oak regeneration. The invasion of oak communities by alien plants also appears to be related to the introduction of livestock. Oaks were more plentiful

before European-American settlement. Habitat was lost to cultivation, and many oak stands were eliminated or thinned to increase forage for livestock. Areas that are open woodlands were once more closed, savannas were woodlands, and grasslands were savannas. Communities now dominated by alien annual grass taxa probably owe their origin to livestock (Baker 1978, Heady 1990). Wetlands are especially attractive to livestock and therefore often are more heavily impacted than other nearby communities (Heady and Child 1994, Valentine 1990). Livestock concentrate their activities in riparian areas, around margins of permanent lakes and ponds, and in and around vernal wetlands. Impacts on mountain meadows can remain visible for decades after livestock use has been terminated (Rundel et al. 1990). Livestock can affect the balance between community types along ecotones, e.g., coastal-prairie/coastal-scrub, sagebrush-steppe/conifer-woodland, and sagebrush-steppe/grassland (Heady et al. 1990, Young et al. 1990). Pinyon-juniper woodlands have been treated (trees poisoned or mechanically removed) to enhance forage for livestock (Evans and Young 1987), a process that does not necessarily enhance the habitat for other native plant taxa. Heavy livestock use has changed community composition and structure in some desert communities (Fleischner 1994, Vasek and Barbour 1990).

Livestock herbivory can lead to alterations in species composition of plant communities, ecosystem function, and ecosystem structure (reviewed in Fleischner 1994). Altered species composition can include decreases in densities and diversity of native plant taxa, changing a shrub-dominated community into a grass-dominated one or vice versa. Livestock can destabilize plant communities by aiding the spread and establishment of alien plant taxa, both by transporting seeds and by creating habitat for disturbance-loving alien ruderals. Changes in a plant community affect the animal community (e.g., lack of food and/or cover changes the rodent community, which impacts the predators, etc.). Ecosystem function may be altered through changes in nutrient cycles, water cycles, etc. Livestock grazing always results in a net loss of nutrients, since livestock are exported rather than decomposing in place. In addition, at least some areas in California, like many areas west of the Rocky Mountains, lack organisms necessary for decomposition and recycling of nutrients tied up in cattle and horse feces (see Mack and Thompson 1982). Dried, apparently intact feces can be found several years after removal of livestock (personal observation). Alteration in ecosystem structure can include changes in vegetation stratification, increases in soil compaction, and loss of soil stability (Fleischner 1994). Loss of plant cover, soil crusts, and litter can increase loss of soil to erosion. Loss of plant cover, together with decreased water infiltration

tion (related to soil compaction) can contribute to flooding and gullying. Cryptobiotic soil crusts are essential to ecosystem function and structure in semi-arid and arid ecosystems (Fleischner 1994). These crusts are composed of cyanobacteria, lichens, and mosses, and are associated with increased organic matter, available phosphorus, increased soil stability, increased soil moisture, and enhanced seedling establishment. Cyanobacteria (both free-living and in lichens) fix nitrogen, and can be the dominant source of this limiting nutrient in arid systems. Livestock trampling can greatly damage or destroy these crusts.

Livestock are allowed on public lands in California, on federal, state, regional, county, municipal properties, from national parks to municipal watersheds. Nearly 45% of California is federal land (Jacobs 1991). Environmental Assessments and/or Environmental Impact Studies are often required before grazing can be initiated on public lands and before expired leases can be renegotiated. Such documents need to be carefully reviewed by an informed public. While many are well written, well researched documents, others base management plans on popular (but scientifically unsubstantiated) concepts (e.g., Savory 1988).

In terms of negative impacts on native plants, livestock herbivory may not be the most destructive land use practice. There are a lot fewer native plants in cultivated fields and manicured lawns than in grazed savannas. Although it is not true for most of the western United States, in the more desirable parts of California much of what is now used for livestock might be lost to subdivisions and development—sometimes the choice is cows or condos (see Wuerthner 1994c).

Careful consideration of alternative land uses needs to be made before an end to grazing is called for. Many of the negative impacts of grazing can be mitigated with careful, well planned management. In areas where livestock herbivory is going to continue, selection for damage tolerance might allow for increased success in revegetation with natives. All management decisions have consequences. Abrupt changes in livestock herbivory can bring new problems, e.g., a major increase in *Foeniculum vulgare* on Santa Cruz Island when cattle were removed (Junak et al. 1995).

While herbivory probably is a natural part of all terrestrial ecosystems, livestock herbivory is not a natural part of California natural ecosystems. Livestock behavior does not mimic that of either Pleistocene or modern native California herbivores (Baker 1992). It must be viewed as a human-imposed alien disturbance and be carefully managed to minimize negative impacts. That said, there is a place for carefully managed livestock in California, particularly on private land. The livestock industry is significant both economically

and culturally, and, if carefully managed, it can help maintain open space and a place for much of the native flora that would be lost with other land uses.

ACKNOWLEDGMENTS

I would like to thank Dirk Van Vuren and Christine Schonwald-Cox for providing information and advice, Dieter Wilken for useful comments on the manuscript, Susan D'Alcamo for involving me, Katherine Culligan for all her help before the symposium, and Margriet Wetherwax for the final impetus.

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(Received 3 Feb 1995; accepted 3 Feb 1995)

FLORISTIC INFORMATION SYSTEM FOR CALIFORNIA TRACHEOPHYTES (FISCT)

THOMAS J. ROSATTI and THOMAS DUNCAN
Jepson Herbarium and University Herbarium
University of California, Berkeley, CA 94720

ABSTRACT

In this paper a plan is outlined for the long-term development of an electronic, network-accessible Floristic Information System for California Tracheophytes (FISCT). FISCT is both an extension and an application of the Specimen Management System for California Herbaria (SMASCH), and will serve as an interface between SMASCH and future, electronic versions of *The Jepson Manual*. It is an extension of SMASCH in the sense that its initial development is occurring within the SMASCH project at UC Berkeley, in conjunction with efforts to provide—through the construction of electronic, multiple-entry keys—identifications of California plant material to be included in the SMASCH database. In the future, development of MEKA keys for FISCT will be undertaken mostly by contributors to *The Jepson Manual*, in connection with their efforts to annotate specimens belonging to and revise treatments of the groups for which they are authors. Thus, FISCT will comprise MEKA keys to the taxa of vascular plants occurring without cultivation in California, and eventually will include for each, via electronic versions of *The Jepson Manual*, dichotomous keys, morphological as well as ecological descriptions, and digitized illustrations. FISCT is an application of SMASCH in that it will rely on that system for accession-level data, including but not limited to nomenclatural histories, the citation of relevant literature, elevational ranges and geographic distributions. Ultimately, each accession record in the SMASCH database will be connected by its geographic coordinates to digitized maps of California, enabling nearly instantaneous display of distributions as well as checklists, based on whatever annotations users wish to specify. FISCT will serve as an interface between SMASCH and *The Jepson Manual* once the latter is put into machine-readable form and connected electronically to the SMASCH database.

Botanists and others have been speculating, at least informally, about the potential advantages of electronic floras for some time now. Among other things, most observers agree that they would enhance the general flow of information about plants and that they would be much more readily corrected and updated than their paper-based counterparts have been. Nevertheless, it was apparent to us in attending the session “Flora of the World, Current Knowledge and Future Prospects” at the recent International Botanical Congress in Yokohama that little has been done to implement the ideas and to make use of the technology involved; participants discussed various floristic projects throughout the world, including a world flora (*Species Plantarum*), yet mentioned the application of networked information technology only in passing or did not consider the subject at all.

In this paper a plan is outlined by which data about the flora of California will be distributed electronically over computer networks. It involves the SMASCH project and its accession-level data on one hand (Bartholomew and Duncan 1992; Duncan et al. 1993; Rosatti et al. 1994), and *The Jepson Manual* and its information about taxa on the other (Hickman 1993). The plan will require cooperation and collaboration among the SMASCH project, the Museum Informatics Project (MIP), the Jepson Herbarium and Trustees, the University of California Press, the University Library, and the editors and contributors who will be involved in future editions of *The Jepson Manual*. In the electronic format that we propose, the text of *The Jepson Manual* will be much more easily searched and revised, while it and related resources will be available to a larger number of users for a wider range of purposes.

BACKGROUND: MEKA KEYS

As implementation of SMASCH proceeded, we began to develop electronic, multiple-entry identification keys because of practical needs related to our commitment to identify all California accessions in JEPS and UC for the database. In the process, we formulated a plan that would encompass all of the elements that could be regarded as comprising a truly complete, electronic flora, and that could serve as a prototype for others as well.

We currently are using treatments in *The Jepson Manual* to help identify accessions of California plants in JEPS and UC. For genera in which only one species is known to occur in the state, we are using these treatments directly, but for genera in which more than one species is involved, we are using data primarily from *The Jepson Manual* as a starting point in the construction of electronic, multiple-entry identification keys, using the interactive, Multiple-Entry Key Algorithm (MEKA and MEKAEDIT), developed by Duncan and Meacham (1986a, b) and Meacham (1994).

In the development of these MEKA keys, data primarily from *The Jepson Manual* are being used to fill out data matrices in which values of "+" (present in all members of a taxon), "-" (absent from all members of a taxon), "*" (present in at least one but not all members of a taxon), and "?" (condition unknown for a taxon) are entered for each of a string of character states for each taxon. A specimen then may be identified by clicking on character states that apply until the list of possible taxa is reduced to one.

For our purposes, multiple-entry keys are preferable to dichotomous ones in several ways (Tables 1 and 2): they do not require that each of a fixed series of choices be made correctly in order to arrive at an identification; they do not often involve bottlenecks (e.g., steps in dichotomous keys that rely on single structures, such as flowers

TABLE 1. DICHOTOMOUS KEY PATH IN *THE JEPSON MANUAL* AND MINIMUM DIAGNOSIS THROUGH MEKA FOR *CHAENACTIS SANTOLINOIDES* GREENE. In this example, the character states needed to completely distinguish *C. santolinoides* using a minimum diagnosis from MEKA are fewer in number, more easily determined, and more frequently present than those encountered in the key path to this taxon in this dichotomous key to the 20 taxa of *Chaenactis* treated in *The Jepson Manual* (see Hickman 1993, p. 223).

The Jepson Manual (5 key leads, 18 character states):

1. Per (bien?) to subshrubs, rarely fl 1st year; pappus scales (6)8–20 per fr in distinct series, \pm equal; outer corollas radial, not strongly enlarged (sect. *Macrocarphus*).
 2. Pls \pm scapose, cespitose to \pm matted; heads 1(–3) per st; gen subalpine to alpine.
 3. Phyllaries glandular-hairy.
 4. Lf blades linear to elliptic, longest lobe near middle, tips curled to twisted.
 5. Largest lf blades linear to narrowly elliptic, lobes gen > 9 pairs, densely crowded *Chaenactis santolinoides*

MEKA (2 character states):

Longest primary leaf lobes near blade middle, primary lobes of largest leaves gen > 9 pairs *Chaenactis santolinoides*

or fruits, that are not always present); they allow for the determination of minimum diagnoses, which are lists or sets of lists of the fewest numbers of character states needed to completely distinguish a taxon (e.g., a species in a genus); they facilitate the determination of unique character states, which are those that by themselves completely distinguish a taxon; and they may be expanded with respect to both taxa and character states quite readily, with no need for restructuring of any kind.

The advantages of MEKA keys discussed above are of tremendous value to us in meeting our commitment to identify over the next 5 years or so approximately 300,000 accessions of California plants in JEPS and UC. It is much faster and easier to identify a stack of herbarium specimens by determining only one or a few character states for each than it is to perform the same task by having to read through and choose from many more character states in a dichotomous key; of course, the severity of this limitation depends on the length of the key and the position of the taxa within it. In addition, the minimum diagnoses and unique character states in some cases exclude habit, reproductive structures, underground parts, and other features commonly found in dichotomous keys that often are absent or difficult to determine.

Preliminary MEKA keys, which are direct and unedited translations of some of the data from dichotomous keys and descriptions

TABLE 2. KEY LEADS AND CHARACTER STATES ENCOUNTERED IN DICHOTOMOUS KEY PATHS IN *THE JEPSON MANUAL* AND MINIMUM DIAGNOSES THROUGH MEKA FOR EXAMPLES SELECTED FROM GENERA A THROUGH C IN CALIFORNIA. In most of these examples, the number of character states needed to completely distinguish a taxon using a minimum diagnosis from MEKA is fewer than both the number of character states and the number of key leads encountered in the key paths to these taxa in the dichotomous keys in *The Jepson Manual* (see Hickman 1993, pp. 202–203, 215–216, 223–224, 229).

Taxon	Dichotomous key leads in <i>The Jepson Manual</i>	Dichotomous key character states in <i>The Jepson Manual</i>	MEKA character states (minimum diagnosis)
<i>Artemisia tridentata</i>			
subsp. <i>tridentata</i>	11	34	3
<i>Artemisia norvegica</i>			
subsp. <i>saxatilis</i>	6	16	2
<i>Artemisia spinescens</i>	2	8	1
<i>Brickellia arguta</i>			
var. <i>odontolepis</i>	7	14	7
<i>Brickellia frutescens</i>	6	13	3
<i>Chaenactis glabriuscula</i>			
var. <i>megacephala</i>	7	21	3
<i>Chaenactis stevioides</i>	6	27	3
<i>Chrysanthmus nauseosus</i>			
subsp. <i>mohavensis</i>	7	16	3
<i>Chrysanthmus viscidiflorus</i>			
subsp. <i>viscidiflorus</i>	8	16	3

into MEKA format, have been prepared mostly by Data Entry Assistants in the SMASCH project. Once in MEKA format, expressions of the character states in English as well as the values for each taxon with respect to each of these character states are modified, when necessary, as a result of observations made in the process of examining the plant material to be identified, yielding a final MEKA key. In some cases, additional character states are added, from the plants themselves or from various sources in the literature, to complete or strengthen the distinctions among taxa. Thus far we have produced, mostly for Asteraceae in California, preliminary keys for about 80 genera and 450 species and infraspecies, and “final” keys for about 32 genera and 212 species and infraspecies. In the future, others will be involved in this process in that contributors revising treatments for subsequent editions of *The Jepson Manual* will annotate the pertinent accessions in JEPS and UC and produce MEKA keys for their groups as well.

THE PLAN: FISCT

Over the long-term we will develop a complete floristic information system for the vascular plants of California, of which an

electronic version of *The Jepson Manual* will be a most important part, to be accessible over Internet and to be known as the Floristic Information System for California Tracheophytes (FISCT); we expect that within the next five years a functional prototype of this system will be in place. According to our plan, FISCT eventually will comprise electronic, multiple-entry identification keys to the taxa of vascular plants occurring without cultivation in California and will include for each, via electronic versions of *The Jepson Manual*, dichotomous keys, morphological as well as ecological descriptions, horticultural information, and digitized illustrations; each taxon will be represented by digitized photographic slides as well, from the Jepson Slide Collection as well as other sources, of entire plants in their habitats as well as of individual parts critical in identification. For type specimens of these (and other) taxa, we will build an archive within SMASCH of images, including both magnifications and dissections showing critical features.

FISCT will serve as an interface between an electronic *Jepson Manual* and the SMASCH database in that it will rely on *The Jepson Manual* for the elements listed above, in addition to the glossary and other introductory material, while it will rely on SMASCH for images of accession sheets as well as accession-level data including but not limited to nomenclatural and annotation histories, the citation of relevant literature, elevational ranges, and geographic distributions. Ultimately, each accession record in the SMASCH database will be connected by its geographic coordinates to digitized maps of California, enabling nearly instantaneous display of the distributions of taxa in the state as well as checklists of taxa for any area of interest, based on whatever annotations users wish to specify.

Regarding our own annotations, we have kept in fairly standardized form notes regarding the ways individual accessions do not conform to the taxa to which we have assigned them. Thus, for example, users eventually will be able to obtain a point-by-point distribution on a digitized map of all accessions we have assigned to a particular taxon, as well as of all accessions we have assigned to that taxon that have a character state that does not conform to that taxon. In these and other ways, SMASCH will serve as a tool in the evaluation of taxa and patterns of variation for a wide range of purposes.

Staff of MIP have loaded from tape and placed in Interleaf format the entire text of *The Jepson Manual*, and portions of it have been used in collaboration with the staff of the University Library as part of a more general effort to explore the use of Standard Generalized Markup Language (SGML) for processing electronic text. SGML is an emerging standard for encoding text, an important consideration for ensuring long-term viability as well as interoperability via computer networks with systems that will be developed elsewhere in the

world. The development of network applications and the use of standard editing tools for SGML also will facilitate the ongoing correction and revision of *The Jepson Manual*.

In the context of FISCT, the use of SGML markup (which describes the structure or content of a text, not its appearance) in conjunction with a document type definition (DTD) designed for floristic information will allow for the extraction of sections of *The Jepson Manual* based on defined criteria as well as context-based searching of the text. For example, habitat descriptions for specific taxa could be extracted, or occurrences of an idea such as "red flowers" could be identified by searching contexts defined as "flowers," "petals," "corollas," and "stamens" for the word "red" (thus excluding other contexts in which "red" would be irrelevant).

An initial prototype of an electronic version of *The Jepson Manual* has been created using as sample text the family description and treatments of the first nine genera of Asteraceae (*Acamptopappus* through *Agoseris*). The user interface employed in this prototype is the Dynatext Browser (Electronic Book Technologies, Inc.), a system for electronic publishing that provides formatting as well as searching capabilities based on SGML markup. For the prototype, contexts including but not limited to description, chromosome number, commonness and rarity, habitat, elevation, geographic range, and horticultural value have been encoded, making it possible to search this entire document or specified parts of it for values of interest within them. For example, the command in Dynatext's query language "<habitat> cont juniper woodlands" executed on the entire sample document indicates that only the habitat statement for *Acamptopappus sphaerocephalus* contains the words "juniper woodlands." Although it is generally possible to search an electronic version of a text for occurrences of something like "juniper woodlands" or any other string of characters, it is desirable to define contexts (such as "habitat" in this case) for purposes of interoperability and in order to exclude occurrences of a given string of characters that are considered irrelevant to the question being asked.

The Dynatext prototype also includes a "table of contents," which lists the taxa included hierarchically and allows a user to go instantly to any desired treatment by simply clicking on the appropriate taxonomic name; the results of searches are also displayed numerically, by taxon, in this list. Another feature built into the prototype is a mechanism whereby clicking on a scientific name in a dichotomous key sends the user to the treatment of the corresponding taxon. Finally, some of the smaller illustrations have been embedded in the text in appropriate places, while the larger ones, in addition to digitized photographic slides, are brought onto the screen by clicking on icons.

Eventually, we will connect our MEKA keys and the text of *The Jepson Manual* to a fully illustrated glossary, so that by merely

clicking on a word of unknown or uncertain meaning a user will be provided with a pop-up definition and accompanying picture. We believe that such a tool, in addition to other mentioned advantages of electronic keys and floras in general, will result in more accurate identifications of plant material, particularly by non-specialists, and might even render the prospect of identifying plants less formidable to those with budding interests in the field. Of course, we would caution users that in critical cases, as with any floristic work, other types and sources of information should be consulted for confirmation.

CONCLUSIONS

Our goal is to make various kinds of floristic information available in electronic form, for use in herbaria, libraries, offices, homes, and even in the field (using hand-held computers). We also expect that in the near future, in addition to coordinates for collection localities determined by a geographic positioning system (GPS), a person in the field will be able to enter other collection data into hand-held computers for later input into databases and production of collection labels.

The plan discussed here was not developed in isolation, and its implementation will not proceed without cooperation and collaboration with others. With regard to accession-level data, SMASCH was developed with input from throughout the community of expected contributors and users, and its implementation will continue to proceed in close association with the California Academy of Sciences and the Rancho Santa Ana Botanic Garden. Representatives from major institutions in New Mexico, Arizona, Oregon, Washington, Nevada, and Hawaii are preparing grant proposals involving the use of SMASCH for their collections, and have held discussions with us about forming a Western United States Botanical Accession Database Federation. On the floristic side, collaborations will occur that involve the people and institutions mentioned above, and we have been and continue to be in close contact with the Biota of North America Program (BONAP) at the University of North Carolina about how FISCT will mesh with their plans for a floristic information system for North America north of Mexico.

The system we envision will not only store, manage, and distribute information about the flora of California, it will also serve as a research tool in the generation of such data by monographers and floristicians. Accession-level data, a major source of the information on which taxonomic and floristic information is based, will be more accessible and better managed in the future because of SMASCH, while the ability to evaluate patterns of variation will be dramatically enhanced by digitized mapping and other geographic tools. These and other improvements should result in sounder, more efficiently

produced taxonomic and floristic treatments of California plants in the future.

ACKNOWLEDGMENTS

The plan discussed in this paper would not have been developed without support provided to the SMASCH project by the National Science Foundation, through NSF-BSR-9104156. We thank many people for the contributions they have made thus far. Randy Ballew of MIP and Mickey Ellinger of SMASCH have been responsible for making the hardware and software do what we all think it should. Elizabeth Neese, formerly of SMASCH, provided important insights from her perspective as a field botanist. Courtney Terry and Liza Lewis, both formerly of SMASCH, constructed most of the preliminary MEKA keys. Glen Jackson of MIP resurrected the back-up copies of *The Jepson Manual* and placed them in Interleaf on the MIP server for use in the SGML prototype. Susan Stone of MIP marked-up in SGML the part of *The Jepson Manual* discussed, and has been very helpful in explaining to us what she has learned, in collaboration with the University Library, about this standard for encoding text. Peter Rauch has experimented with Kodak photo CD technology as a way to have photographic slides quickly and inexpensively digitized, and has located substantial sources of such material outside the University for inclusion in FISCT; Brother Eric Vogel of St. Mary's College has offered us the use of about 20,000 slides of California plants from the collections at that institution. We are also grateful to Chris Meacham of MIP for modifying and improving MEKA and to John Kartesz of the Biota of North America Program and Buck Reed of the U.S. Fish and Wildlife Service for discussions about how FISCT will fit into larger plans for an electronic floristic information system for the entire continent.

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(Received 29 Sep 1994; accepted 1 Feb 1995)

THE FUTURE OF CALIFORNIA FLORISTICS AND SYSTEMATICS: COLLECTING GUIDELINES AND DOCUMENTATION TECHNIQUES¹

WAYNE R. FERREN JR.

Department of Biological Sciences, University of California,
Santa Barbara 93106

DAVID L. MAGNEY

Fugro West, Inc., 5355 Olivas Park Drive
Ventura, CA 93001

TERESA A. SHOLARS

Science Department, College of the Redwoods,
Fort Bragg, CA 95437

ABSTRACT

At the Jepson Symposium, a workshop entitled "The Future of California Floristics and Systematics: Collecting Guidelines and Documentation Techniques" was convened on 4 June 1994, to prepare and approve by consensus a series of findings and recommendations that can be used to improve substantially the documentation of the environmental review process and scientific methodology so that preparation and preservation of botanical voucher specimens will become a professional standard. The workshop was attended by fifty-one participants who approved the findings and 14 recommendations in four major areas of concern: (1) documentation of environmental analyses with herbarium voucher specimens; (2) documentation of experimental research with herbarium voucher specimens; (3) presentation of hierarchical data on specimen labels; and (4) what will the future hold for documentation of California's botanical heritage?

Two approaches can be developed for the Jepson Symposium workshop topics "collecting guidelines" and "documentation techniques": (1) How shall investigators of the California flora decide what and when to collect? and (2) What kinds of data shall be recorded that will be presented on the herbarium specimen labels? With the publication of *The Jepson Manual* (Hickman 1993), another question might also be raised by some investigators, "Should we continue to collect the California flora, and if so, how should we go about continuing the effort?"

Because of state and federal requirements for environmental review of proposed development and the regulation of species of special interest and environmentally sensitive habitats such as wetlands, numerous environmental impact reports (EIR's), environmental im-

¹ The executive council of the California Botanical Society, the boards of the California Native Plant Society, and the Association of California Herbaria have endorsed each of the 14 recommendations offered by the participants of this workshop.

pact statements (EIS's), environmental assessments (EA's), and other types of reports are being generated that often record important aspects of the California flora, but that in great majority are not documented by voucher specimens. Without vouchers deposited in institutional herbaria, the scientific and even legal credibility of these reports is suspect at best, and their long-term value is minimal in spite of the large sums of money spent in producing the documents. In southern California, it is not uncommon for approximately \$1 million to be spent for a specific plan and associated EIR for larger development projects.

In another realm of investigation, scientific studies conducted at academic institutions often can be constrained by today's limited funding, which makes impractical the extensive plant collecting associated with broad and often unfocused floristic inventories. Thus another question could be asked, "What can we afford to document with collections and who is going to pay for the maintenance of these collections?" Furthermore, at these same institutions, important laboratory-based and greenhouse-based studies are largely undocumented by voucher specimens, a situation that unfortunately emphasizes the lack of cooperation and even lack of understanding among (1) the more traditionally-trained, organismal field biologists and (2) the laboratory-trained, molecular biologists.

To further compound the issue of documentation, the recently-achieved widespread use of computers in herbaria and the development of software for sophisticated databases, which include specimen label data, have resulted in the need to re-evaluate the type of data presented on labels when collections are made. The frequent lack of hierarchical provenance (purpose or project-related data), geographic, and habitat data sets, or source of experimental material, diminishes greatly the usefulness of the computerization efforts.

The overall need for accurate, detailed documentation of research, be it field-oriented or laboratory-oriented, is perhaps as great as it ever has been. Whether investigators are documenting a plant species in the field or with voucher material for laboratory analyses, the role of herbaria as repositories of preserved specimens and label data is indispensable in the continuing investigation of the California flora. Support for focused projects, whether they are academic or applied, must continue and the documentation of these projects with preserved voucher specimens must be expanded to new areas of investigation.

Concern and even alarm for the lack of professional documentation of academic and applied botanical research fueled our participation in this symposium and our desire to organize the workshop *The Future of California Floristics and Systematics: Collecting Guidelines and Documentation Techniques*. The purpose of this workshop, held at the University of California, Berkeley, on 4 June 1994, was to prepare and approve by consensus a series of findings

and recommendations that can be used to improve substantially documentation of the environmental review process and scientific methodology so that preparation and preservation of botanical voucher specimens will become a professional standard. This purpose is consistent with the overall purpose of the Jepson Symposium, as reported by The Friends of The Jepson Herbarium (Anonymous 1994): . . . The Friends are sponsoring a symposium to explore the challenging opportunities of future research, education, and conservation of California's unique flora. As we move toward the 21st century, a continuing dialogue is essential among interested individuals, agencies, and academics. Only through cooperation and communication can we begin to understand and protect our native plants.

WORKSHOP PROCEDURE

Prior to this workshop, the panelists prepared a draft set of "findings" and "recommendations", copies of which were presented to the workshop participants. Panelists presented introductions to each of four topics, which were followed by discussions from participants. Phone and written polls also were taken by panelists prior to the workshop to provide evidence on the practice of botanical documentation with voucher specimens and on the methods of specimen preparation, if and when vouchers are prepared. Following presentation and discussion of topics, a panelist read the draft findings or recommendations and a motion was made to adopt the findings by consensus. The panelist then called for discussion of the findings or motions and for proposed amendments. Amended findings or recommendations then were adopted by consensus when the earlier motion to adopt was seconded by a workshop participant. We provide a review of participant discussion following each workshop finding and recommendation. The following is a breakdown of the participant affiliations as determined from a workshop register ($n = 51$): academics (37.3%); agencies (9.8%); botanic gardens (9.8%); consultants (7.8%); individuals (11.8%); nurseries (3.9%); and societies (19.6%). This analysis of participants is, however, potentially misleading, because many participants who indicated their primary affiliation to be academic, botanic garden, or society also serve as environmental consultants, and many of the consultants also are affiliated with one or more societies. Nonetheless, workshop participants were overwhelmingly professional botanists who have diverse professional orientations.

FINDINGS AND RECOMMENDATIONS

As a result of the Jepson Symposium workshop entitled *The Future of California Floristics and Systematics: Collecting Guidelines and Documentation Techniques*, the participants by consensus make

the following findings and offer the following recommendations and discussions:

Topic I- Collecting Guidelines: Documentation of Environmental Analyses with Herbarium Voucher Specimens

WORKSHOP FINDINGS: Environmental documents produced as a result of the California Environmental Quality Act (CEQA) and National Environmental Policy Act (NEPA) processes are professionally documented with botanical voucher specimens by a small percentage of the total work conducted by environmental consulting companies. This situation results in the loss of opportunities to substantiate project conclusions and in the loss of botanical information that could be invaluable for subsequent applied and academic studies.

An informal phone poll of ten large to small environmental consulting companies, which was conducted by the chair prior to the workshop, revealed that all but one company collected voucher specimens for less than one percent of the plants listed in their reports, and the tenth company reported the figure to be less than five percent. Of those specimens collected, most consultants reported that they largely collected plants for identification purposes and that the majority of these collections were never deposited in a formal herbarium. These figures and methodology were consistent with the situation experienced by workshop participants. Because participants in this workshop are alarmed at the lack of professional documentation of environmental work, we offer the following recommendations to the environmental community and to local, state, and federal regulatory and advisory agencies:

Recommendation 1. Environmental review projects (e.g., EIR's, EIS's, EA's) that are conducted in the State of California and that include botanical field observations should also include voucher specimens, and/or photographic documentation consistent with existing standards, deposited in one or more herbaria listed in *Index Herbariorum, Ed. 8* (Holmgren et al. 1990).

Perhaps the most extensive debate of the workshop centered around the extent to which all environmental reports should be documented by botanical voucher specimens and whether or not it was acceptable to deposit only photographs of particularly rare taxa or populations. Consensus by participants that environmental review projects should be documented by vouchers demonstrates the importance we place on botanical documentation and the need to improve current practices. Only when a particular taxon is determined to be too rare or endangered to collect a voucher specimen should a photograph be used as a voucher. For genera with many species, a photograph may

not provide sufficient information for someone to determine independently the identity of a taxon.

The role of various types of herbaria may differ regarding the issue of accepting vouchers for environmental reports. The panelists conclude that because many small herbaria are not listed in *Index Herbariorum*, voucher specimens deposited in these herbaria may not be available to a wide range of interested parties. Thus small herbaria that wish to serve as repositories for vouchers should become listed formally. The role of herbaria at public versus private institutions was raised by a reviewer of this paper, who pointed out that two of the three major herbaria in California are private and their role and the role of other private herbaria could be quite different in the responsibility of accepting vouchers, particularly those mandated by legislation. This reviewer also raised the concern as to whether a particular herbarium would have the alternative to accept in total, in part, or not at all a particular set of specimens generated from an environmental study. These issues, concerns, and questions regarding the role of various herbaria warrant additional discussion at a statewide level.

Recommendation 2. The thoroughness of documentation for a particular project should be equivalent to the importance of the study, but in any case should include collection of voucher specimens for special status species studies and noteworthy botanical observations (e.g., range extensions; state and county records; rediscoveries).

Much discussion was directed toward the extent to which project checklists should be documented. Should all plants listed in a report be documented by a voucher specimen? What is meant by the importance of a project? There was agreement that a purposefully vague recommendation would provide project reviewers with regulatory authority the flexibility to make individual determinations about specific projects. In some cases, entire checklists might warrant documentation with voucher specimens, whereas others might warrant documentation of only noteworthy observations. Weedy taxa (e.g., *Taraxacum officinale*) or more obvious locally common taxa (e.g., *Sequoia sempervirens*) might not have to be collected. A notation such as an asterisk could be made by each unvouchered observation. In any case, it was suggested by some participants that importance of a project should be considered a measure of project complexity and scope.

A reviewer of this manuscript also suggested that the length of time certain vouchers must be kept is another area for consideration. Rather than in perpetuity, vouchers for some projects could be maintained for a particular length of time while the legal technicalities of the project are under review, but might not necessarily be main-

tained after the legal process has gone to completion. This approach apparently is practiced currently by some consulting companies. The end result of only temporarily preserving vouchers at institutional herbaria or in corporate collections, however, is the eventual loss of material for future systematics studies and the loss of potentially important information on a site's botanical diversity, as well as the future inability to check for the accuracy of plant identifications and distribution records presented in the environmental reports.

Recommendation 3. Clients (e.g., private or public permit applicants) for whom environmental studies are conducted should be held financially responsible for the collection, identification, and curation of botanical vouchers; otherwise there is little chance that the current lack of documentation will improve.

For a little extra money, a much more worthwhile review effort could be undertaken. A client's money would be more wisely spent if vouchers were collected and deposited in a formal herbarium than if the environmental review was not documented professionally. During the phone poll taken by the workshop chair, all consultants indicated they or their subcontractors would be willing to collect and label voucher specimens if their employers (project proponents) included the activity in contract scopes of work and also included a budget category for voucher specimen collection, preparation, and curation. Workshop participants emphasized that since the overall budgets for major environmental review studies and documents are substantial, it would take only a modest addition to the budget to cover the costs of collecting and depositing voucher specimens.

Recommendation 4. Collection of botanical vouchers and the deposition of them in formal herbaria should be a requirement of the CEQA and NEPA processes. We recommend that the responsible agencies and legislative bodies undertake a review of state and federal legislation and make appropriate amendments that will result in the collection and preparation of botanical vouchers becoming a formal part of the environmental review process.

Although the workshop participants realized that these recommendations have no particular legal status, there was agreement that any influence that resulted in an improvement in the documentation process could enhance greatly the validity of the environmental review process.

Probably the most important point to remember about CEQA is that it is a law enforced by the public. That is, no government body has the authority to oversee and regulate implementation of CEQA; rather, it is the public's responsibility to "regulate" the environmental review process and "make" the lead agency fulfill the intent of this full disclosure law. If the botanical community is not satisfied

with the botany sections of EIR's because they are not supported by voucher specimens, CEQA documents may be ripe for criticism.

Professional standards are generally applied as the guidelines to follow by each profession. For example, cultural, historic, and paleontological sites are all recorded and submitted to databases as part of the CEQA and NEPA review processes because sites containing these resources are considered important by archaeologists, historians, and paleontologists, respectively.

The panelists and workshop participants, many of whom are botanists, also consider the botanical resources of a site to be important and we think these resources should receive appropriate levels of documentation, including the collection and curation of voucher specimens.

Topic II- Collecting Guidelines: Documentation of Experimental Research with Herbarium Voucher Specimens

WORKSHOP FINDINGS: Although there is continuing growth in experimental botanical research, particularly at the molecular level, many if not most experimental research projects are not documented with voucher specimens deposited in formal herbaria. In what may be interpreted as an expanding gap between herbaria as repositories for scientific vouchers and the experimental academic as well as the applied biological communities, herbaria are often left to defend themselves against a declining user base.

As participants in this workshop, we find the lack of documentation with vouchers to be alarming. Goldblatt et al. (1992) in their article Documenting Scientific Data: The Need For Voucher Specimens state that, "Vouchers are central to any serious questioning or reexamination of data and conclusions. An unexpected result may be due to convergence or to past misinterpretation of morphology and other characters, but it may also be caused by misidentification of the plant examined."

Ecological studies are not immune from the practice of not documenting taxa in studies. Recently, one of the authors, T. Sholars, gave a seminar on the "Vegetation and Flora of Mendocino County's Pygmy Forest" to a group of scientists whose research site was in the Pygmy Forest. During the slide presentation of the common plants, it was discovered that the researchers had misidentified *Myrica californica* (Myricaceae), one of the taxa from which chemical extractions had been taken, as *Heteromeles arbutifolia* (Rosaceae).

We offer the following recommendations to the scientific community and to academic institutions that support herbaria.

Recommendation 5. Preparation of botanical voucher specimens should be encouraged as an important part of the scientific process.

Institutions and departments that house or otherwise support herbaria should develop policies regarding the deposition of vouchers by students, staff, and faculty. Support for herbaria should come not only from the host institution or department, but also from the users who deposit specimens. Agencies or corporations that fund research should be made aware of the importance of voucher specimens and should request that the preparation and curation of vouchers be included as a regular part of proposals and budgets.

Quoting again from Goldblatt et al. (1992), "Absence of a voucher makes it impossible to reassess identity. To avoid potential future problems, we suggest that leading scientific journals insist on the citation of an existing herbarium voucher and an indication of its location. Absence of a voucher for critical taxa should be explained so that readers are somehow assured of the identity of the study materials."

A workshop-proposed policy for scientific journals to require the collection and deposition of voucher specimens that provide documentation for published papers also received strong support, but was not part of this approved recommendation. It was noted that too many papers are published with no mention as to whether vouchers were prepared or in which repository they are housed. There was agreement that if specific voucher specimens were not cited by collector, collection number, and institution, at least a mention of the institution in which all specimens were deposited would be an important improvement over the current situation.

Recommendation 6. Academic institutions should include in their curricula opportunities to expose all students to the importance of scientific documentation and the need to prepare and preserve botanical and other biological voucher specimens. There is an urgent need to educate students in the importance and functions of systematics collections whether these students anticipate a future in academic or applied science or want to be well-rounded citizens concerned with California's natural resources or experimental processes.

Workshop participants stressed the need for researchers and students to work cooperatively with peers of many disciplines. Many students are no longer trained in many traditional areas of science, and thus they are not exposed to the need for and process of scientific documentation with voucher specimens or the preservation of archival materials for applied or academic projects. Besides putting scientific accuracy at stake due to the lack of voucher specimens, this can result in the under-utilization of herbaria at academic institutions, because fewer professions refer to or deposit specimens in these herbaria not because it is unnecessary but because the re-

searchers have not been trained to do so. The broad reduction in the support of systematics collections in general, which comes oddly enough at a time when there is an increasing interest in biological diversity, is not because of a reduced need for systematics collections such as herbaria, but because there is a reduction in the understanding of the importance of these collections and the programs associated with them.

Topic III- Documentation Techniques: Presentation of Hierarchical Data on Specimen Labels

WORKSHOP FINDINGS: Many herbarium specimens lack clear and complete hierarchical geographic and habitat data that generally make such specimens less useful for a wide range of studies. Because of the increasing accessibility of computers, programs, and networks, there is an increasing ability to make use of many forms of hierarchical data that can be associated with herbarium specimens.

The primary purpose of locational data on herbarium labels is to provide evidence as to where the plant was growing so that the site could be revisited if desired. If the label does not provide enough information to relocate the site, it has reduced value. Hierarchical data are building blocks of information that are more specific with each level. For example, a label stating that a plant was found in California doesn't tell you much. At the other extreme, a label stating that a plant was collected at Dry Lakes Ridge doesn't tell much either, unless you have a priori knowledge that Dry Lakes Ridge is in the western Transverse Ranges of Ventura County, California. Additional locality data such as "300 m west of Hwy. 33 at milepost 14.38; elev. 3,825 feet," pinpoints the collection site precisely.

The results of a written survey questionnaire answered by 18 individual consultants from 11 consulting firms as part of this workshop indicate that most respondents provide locality and habitat data on their voucher specimen labels. However, few respondents routinely provide complete hierarchical locational data or habitat data. Fewer respondents regularly provide phenological or population size data. Lack of time, as a result of an inadequate project budget, was the reason identified most commonly for sparse label data.

Recommendation 7. Herbarium specimen collectors and label preparators should take every opportunity to include a wide range of hierarchical data on specimen labels, consistent with existing standards, that will increase the usefulness of specimens and will make access to the information possible through computerization of label data.

The most useful presentation of locational data is to start with the general (coarse-scale) and then provide successively more specific location information. By providing locational data on labels in this manner, a user can obtain these data at whatever level of detail is needed. This format also lends well to computer data entry. The database can then be used to retrieve individual variables or sets of variables, to produce floristic checklists, print labels, and conduct biogeographical research. However, it was noted at the workshop that it is better to have specimens that document the resources of a site, or that document a project regardless of the detail of the label data, than it is to have no specimens at all. Individuals should be encouraged to provide accurate and detailed data, but should not be made to feel inadequate because they have failed to provide detailed label data according to rigorous professional standards.

Recommendation 8. One category of hierarchical data associated with herbarium specimens should be that which (1) identifies the project for which the specimen serves as a voucher, (2) lists the client, agency, and/or institution associated with the project, and (3) names the report in which the specimen is cited.

To identify properly a specimen with a specific project, the collector needs to supply the project name, project proponent or land owner, lead agency, and title and date of the report in which it is cited. These data can easily be presented in the specimen label as headers (titles) or footers (footnotes). If numerous labels are needed because many specimens were collected, preprinted labels with these data or computer-generated labels can save time and money.

Recommendation 9. Investigate the feasibility of integrating voucher specimen label data with computerization efforts such as the Specimen Management System for California Herbaria (SMASCH) to provide mechanisms for biogeographical and floristic studies.

Significant advances have been made in the last few years in the areas of data management and spatial analysis with computer and satellite systems that have direct applications to floristic research. Accurate locational data can be easily obtained from geostationary satellites using Global Positioning System (GPS) units and storing these data, along with any point, line, or spatial attributes desired, and creating an interactive geographic information system (GIS) database. GPS can be useful during field work to determine accurately (and relatively easily) the site location, including site elevation. GIS can be an invaluable tool to assist researchers in analyzing spatial attributes of a site and can be used to study floristics, especially if the SMASCH database is linked to it. For example, the distribution, edaphic, geological, and climatic variables of a partic-

ular taxon can be studied simply by downloading records of herbarium specimens into a GIS that has topographic, geologic, soils, vegetation, and climatic data layers. Queries are then developed to look for environmental patterns that may explain or give clues to distributional pattern.

Topic IV- What Will the Future Hold for Documentation of California's Botanical Heritage?

WORKSHOP FINDINGS: The changing nature of the political and economic world has direct implications for the future of California's botanical heritage and for the methods we use to document this heritage. There is a greater need than ever (1) to provide support for documentation centers such as herbaria, botanical gardens, libraries, organizations, and agencies; (2) to have coordination of activities among those organizations interested in the documentation and preservation of the botanical heritage; and (3) to strengthen and expand support for academic programs that will educate future generations of professionals who will have an even greater demand on their abilities to document and preserve natural resources such as the state's botanical heritage.

The participants of the Jepson Symposium offer the following recommendations to the responsible parties:

Recommendation 10. The Association of California Herbaria (ACH) should take an active role in organizing support for and preservation of California's herbaria.

In the Bylaws of ACH, the following purpose of the organization is stated: "The Association is organized under the General Nonprofit Corporation Law of the State of California for purposes of (1) promoting the development and use of California herbaria, (2) effecting cooperation among California herbaria, and (3) increasing the awareness of the value of these herbaria for a) maintenance and management of botanical diversity, b) research in taxonomy and evolution of plants, and c) training and education concerning plant resources." There is an urgent need to fulfill this purpose to assist with the conservation of the State's botanical resources, many of which are threatened or endangered.

Recommendation 11. The Association of California Herbaria, the California Native Plant Society (CNPS), and the California Botanical Society (CBS) should coordinate their activities toward (1) preservation of California's botanical heritage; (2) long-term support for California's botanical education and documentation centers; and (3) improved documentation of California's botanical resources through implementation of statewide policies regarding the collection, prep-

aration, and curation of voucher specimens for academic and applied environmental and experimental botanical studies.

This workshop convened by The Friends of the Jepson Herbarium is perhaps the most opportune time to provide a focus for this recommendation. Two panelists for the workshop, Wayne R. Ferren Jr. and David L. Magney, are presidents of CBS and CNPS, respectively. Furthermore, Brent Mishler, who is Director of the Jepson and University Herbaria, is Chair of the Executive Committee of ACH. Participants in the Jepson Symposium and this workshop urged officers of these organizations to take a lead in the coordination of standards for botanical collecting and documentation.

Recommendation 12. Local, state, and federal agencies should strengthen and expand (1) their requirements for documentation of environmental reports, particularly in the requirement for voucher specimens; and (2) their relationship with academic institutions and organizations (e.g., ACH, CNPS, CBS) to assist with the professional documentation of environmental work and with the education of future agency staff and consultants; and (3) their support for herbaria that house voucher specimens, which document the botanical resources of public lands and which document the disclosures in reports required by the CEQA and NEPA processes.

Environmental documents prepared under CEQA/NEPA would be improved if they were supported by voucher specimens, and would substantially increase the knowledge of California floristics simply by greatly increasing the volume of plant collections deposited in public herbaria. Furthermore, the quality of botanical collections would likely improve if the agency or consulting botanist knew their work would be scrutinized. Many environmental documents prepared to date under CEQA or NEPA contain extensive checklists of unsubstantiated observations of plants. Without supporting voucher collections, these checklists have no scientific value because they cannot be verified. The panelists and many of the workshop participants have seen one or more lists that contain doubtful observations. Only voucher specimens provide adequate evidence of findings to the scientific community and public at large.

Recommendation 13. Regulatory agencies and other responsible parties should consider developing a formal inter-relationship between (1) agencies or their consultants and (2) academic institutions or museums, whereby the institutions would provide for fee the botanical documentation portion of environmental reviews. Such an arrangement would reduce or eliminate any burden public agencies or private corporations might anticipate from collecting and

curating botanical voucher specimens, while insuring the collection and preservation of important specimens.

Some concern was expressed during the workshop that this recommendation might result in the exclusion of small, independent, botanical consulting companies from performing botanical documentation. The panelists indicated that such an interpretation was never intended, particularly because the best ratio of specimens collected to plants reported is generally achieved by the smaller firms that often serve as subconsultants to larger corporations or agencies. The recommendation does suggest that there can be a way to achieve an improvement in botanical documentation by developing relationships with academic institutions that have formal herbaria, especially if botanical expertise is not available at the desired level of authority from private consultants.

Recommendation 14. The academic institutions of California should continue and expand support for botany programs and herbaria because the documentation and preservation of California's botanical heritage and the future of botanical research contributions depend upon the education of scientists, resource managers, planners, and consultants who have strong backgrounds in professional botanical training.

A discussion by panelists and participants alike focused on the lack of botanists trained to conduct inventories and to prepare voucher specimens of California's flora. Examples of jobs now available in the field of environmental consulting were plentiful; however, there are not enough qualified botanists to satisfy the current job market. For example, timber harvest plans require botanical inventories of rare species on lands under the jurisdiction of the U.S. Forest Service. However, there are not enough professionally-trained botanists within the agency (and other agencies) or among those applying to agencies to conduct the studies.

One of the reasons for the lack of adequately-trained personnel is that many universities and colleges have decreased or eliminated their basic offering in plant taxonomy and systematics. In an additional blow to academic programs, funding for herbaria and other systematics collections has been one of the first items to receive cuts or elimination, and at some institutions, herbaria have been closed and/or transferred to other institutions. To fulfill the state and federal mandates to protect our natural resources, it is imperative that academic institutions return to training qualified botanists to do basic inventory work. This need may never have been more apparent than now, as the nation embarks on a National Biological Survey, the results of which may help guide national and state policy regarding natural resources for years to come.

ACKNOWLEDGMENTS

We thank the many and varied participants of this workshop for their enthusiastic response and sincere interest in the topics discussed at this Jepson Symposium workshop. We thank The Friends of the Jepson Herbarium for sponsoring this Symposium and for inviting us to organize a workshop on botanical collecting and documentation. We also thank the Editor and the California Botanical Society for providing the opportunity to publish the results of this workshop, and an anonymous reviewer of the draft manuscript for raising additional issues and concerns.

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(Received 24 Aug 1994; accepted 4 Nov 1994)

RESEARCH NEEDS FOR CONSERVING CALIFORNIA'S RARE PLANTS

MARK W. SKINNER AND DAVID P. TIBOR

Rare Plant Program, California Native Plant Society,
Sacramento, CA 95814

ROXANNE L. BITTMAN

Natural Heritage Division, Department of Fish and Game,
Sacramento, CA 95814

BARBARA ERTTER

Combined Herbaria, University of California at Berkeley,
Berkeley, CA 94720

TIMOTHY S. ROSS AND STEVE BOYD

Rancho Santa Ana Botanic Garden,
Claremont, CA 91711

ANDREW C. SANDERS

Herbarium, Department of Botany and Plant Sciences,
University of California at Riverside, Riverside, CA 92521

JAMES R. SHEVOCK

Division of Fisheries and Wildlife, USDA Forest Service,
San Francisco, CA 94115

DEAN WM. TAYLOR

Biosystems Analysis,

303 Potrero St., Suite 29-203, Santa Cruz, CA 95060

ABSTRACT

California's is the largest state flora in the nation. Because of California's high level of plant endemism, rich agricultural heritage, and burgeoning human population, the state has more rare and endangered plants than any other. Lack of knowledge about some of these plants limits their conservation: taxonomic and distributional uncertainty often precludes active conservation, since dubious or poorly known taxa are a lower conservation priority and resources for conservation efforts are scarce. For two reasons this predicament is more extreme in California than elsewhere. First, on a strictly proportional basis, large floras are less well known. Second, much of the flora is young and evolving rapidly (or was before human interruption), resulting in limited morphological and genetic divergence and reproductive isolation among closely related plants. Many taxonomic treatments are consequently unstable: rare variants are relegated to taxonomic synonymy by one author only to be recognized by later authors, or vice versa (Edwards and Clinnick 1993). During preparation of the fifth edition of the California Native Plant Society (CNPS) *Inventory of Rare and Endangered Vascular Plants of California* (Skinner and Pavlik 1994), the editors identified over 150 instances of taxonomic and distributional uncertainty which might be clar-

ified by carefully designed systematic and field studies. Further investigation has revealed many others. All are presented here, along with a compendium of California's extinct plants, some of which have potential to be rediscovered. California botanists can help alleviate botanical uncertainty by undertaking appropriate biosystematic or field studies that focus on problematic groups or taxa within California's rare flora. We suggest that the CNPS Rare Plant Program's Rare Plant Scientific Advisory Committee is the ideal agent to coordinate and track systematic and distributional studies of California's rare plants. The Rare Plant Program already maintains active databases tracking progress on the rare plant information needs in California, and CNPS is introducing a new grant program focusing on fundamental rare plant research in California. The involvement of other institutions is encouraged. In particular, faculty members at teaching institutions can contribute through appropriate guidance of graduate research. We urge California's botanical community to participate in these efforts and contribute to better understanding and enhanced protection of California's rare and endangered flora.

Research on rare and endangered plants takes many forms. Among the more stimulating are studies of rare plant population demographics (Pavlik and Barbour 1988), factors limiting rare plant establishment, persistence, reproduction, or reintroduction (Nickrent and Wiens 1989; Pavlik et al. 1993), population genetic diversity and its relationship to endemism, rarity, and conservation (Kress et al. 1994, Soltis et al. 1992), rare plant origins or relationships (Gottlieb 1973, 1974), effects of exotic plants and animals on endangered plants (Clark et al. 1990; Davis and Sherman 1992), and population viability analyses (Menges 1991). Much of this research is funded by state and federal agencies to support the conservation or recovery of legally protected species, and its legacy is a better understanding of the ecology and conservation needs of some of the hundreds of rare and endangered plants in California and the rest of the nation. Nevertheless, existing studies of a few endangered plants must not obscure the reality that most rare plants have not been studied at all, especially with respect to information fundamental to establishing priorities for their conservation (Parnell 1993). This information includes distribution and habitat preferences, degree of differentiation from close relatives and appropriate taxonomic rank, and the presence and extent of natural hybridization.

This is significant since lack of information or disagreement about the taxonomy or distribution of rare plants is frequently an impediment to their conservation (Messick 1987). Land managers and resource professionals are understandably reluctant to expend time and money conserving taxonomically questionable or poorly known taxa, because further research may show that these plants do not merit scientific recognition or are more common than previously thought. As the plant conservation crisis intensifies and conservation resources dwindle, conservationists increasingly must rely on accurate information to establish conservation priorities.

Lack of information is especially acute in California because of its large flora (over 6000 native taxa) and preponderance of rare

endemics (Stebbins and Major 1965), many of which are still in the process of diverging from common ancestors and are hence poorly separable from sister taxa. The presence of so many taxa which vary in geographically complex ways (e.g., *Astragalus lentiginosus* and its many endemic varieties) and typically hybridize at zones of contact or with closely related taxa (e.g., many rare *Lilium* species) means that in many cases circumscription of taxa and definition of their ranges is difficult and requires intensive effort rather than casual surveys.

The recent publication of two significant botanical reference works in California has highlighted much of what we do and do not know about California's rare flora, and stimulated preparation of this paper. *The Jepson Manual* (Hickman 1993; hereafter called the *Manual*) is the first comprehensive flora for California since *A California Flora and Supplement* (Munz and Keck 1973). The fifth edition of the California Native Plant Society (CNPS) *Inventory of Rare and Endangered Vascular Plants of California* (Skinner and Pavlik 1994; hereafter called the *Inventory*) contains information on the distribution, ecology, and conservation status for all the plants in California judged to be rare, threatened, or uncommon. The *Manual* summarizes much of what we know about the California flora as a whole, while the *Inventory* is widely considered the standard reference for California's plant conservation efforts. Each of these references, and the State of California's Natural Diversity Data Base (NDDB) of locations and status of rare and endangered taxa and natural communities, notes numerous instances of uncertainty about the taxonomic recognition, ecology, or distribution of certain of California's more than 1740 taxa of rare plants.

COORDINATION OF RESEARCH

Our purpose here is to summarize this considerable uncertainty, and catalogue opportunities for fundamental research and study that can facilitate rare plant conservation in California. We have organized this summary of research needs for California's rare flora into three categories, each represented below by an information table. The first category is taxonomic uncertainty (Table 1); the second, distributional uncertainty (Table 3); and the last lists the extinct plants in California (Table 4), many of which require immediate field work to ascertain if they can be rediscovered given sufficient effort. Taxonomic circumscription and plant distribution are clearly not independent; since different taxonomic schemes and concepts dictate different distributions for the plants involved, those cases where both taxonomy and distribution are uncertain are listed in Table 1.

We urge interested botanists to use this compilation to focus their

TABLE 1. COMPILED OF TAXONOMIC RESEARCH NEEDS FOR THE RARE FLORA OF CALIFORNIA. Criteria for inclusion are discussed in the text. "Uncertain distinctiveness" means that taxonomic limits are unknown and taxa in question may or may not merit formal recognition. "Uncertain circumscription" means that taxa are distinctive and probably do merit taxonomic recognition, but taxonomic limits are vague or unknown. Rare plants with significant taxonomic and distributional questions are included here rather than in Table 3. Consult Hickman (1993), Skinner and Pavlik (1994), and the CNPS Rare Plant Program for more information about each entry. ^{JM} Author(s) of *The Jepson Manual* treatment. * Research completed, but not yet published. † Deceased.

Scientific name	Authorities	Research problem
<i>Achnatherum lemmonii</i> var. <i>pubescens</i>	Mary E. Barkworth ^{JM} /Beecher Crampton	Uncertain distinctiveness from var. <i>lemmonii</i> , as all known var. <i>pubescens</i> co-occur with typical variety. Some populations show uncertain distinctiveness from <i>A. microphylla</i> , leading to uncertainty about range.
<i>Agrostis hendersonii</i>	M. J. Harvey ^{JM} /James D. Jokert	Uncertain distinctiveness from var. <i>aequalis</i> .
<i>Alopecurus aequalis</i> var. <i>sonomensis</i>	William J. Crins ^{JM} *	Uncertain distinctiveness from <i>A. aequalis</i> . Uncertain taxonomic status of occurrences from Napa Co.
<i>Arabis modesta</i>	Reed C. Rollins ^{JM} /Linda Ann Vorobik*	Relationship to <i>A. macdonaldiana</i> needs formalization.
<i>Arabis oreogena</i>	Reed C. Rollins ^{JM} /Linda Ann Vorobik*	Uncertain relationship to Baja California plants of same name.
<i>Arabis serpentinicola</i>	Reed C. Rollins ^{JM} /Linda Ann Vorobik*	Some plants seem intermediate to <i>A. discidea</i> .
<i>Arctostaphylos peninsularis</i> ssp. <i>peninsularis</i>	Philip V. Wells ^{JM} /Jon E. Keeley	Uncertain circumscription from <i>A. chilensis</i> .
<i>Arnica venosa</i>	Theodore M. Barkley ^{JM} /James D. Jokerst/Steven J. Wolf/William Gruezo	Plant possibly extinct; only remaining occurrence may be an undescribed form of <i>A. serenana</i> .
<i>Aster lenticus</i>	Geraldine A. Allen ^{JM}	Uncertain distinctiveness from <i>B. macrolepis</i> var. <i>platylepis</i> .
<i>Atriplex tularensis</i>	Dean W. Taylor * & Dieter H. Wilken ^{JM} /Kathy E. Freas & Dennis D. Murphy/Hilda Flores/Howard Stutz & Ge-Lin Chu	Uncertain distinctiveness of synonymized rare taxa (e.g., <i>B. higginsiae</i>).
<i>Balsamorhiza sericea</i>	David J. Keil ^{JM} /W. A. Weber	Uncertain circumscription from var. <i>namum</i> .
<i>Berberis fremontii</i>	Michael P. Williams ^{JM} /Andrew C. Sanders/Alan Whittemore	
<i>Blennosperma namum</i> var. <i>robustum</i>	Robert Ornduff ^{JM}	

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Calamagrostis crassiglumis</i>	Craig W. Greene TM	Uncertain distinctiveness from <i>C. stricta</i> ssp. <i>inexpansa</i> and <i>C. nutkaensis</i> .
<i>Calycadenia villosa</i>	Robert L. Carr & Gerald D. Carr ^{TM*} /Bruce G. Baldwin & Susan J. Bainbridge	Probably consists of northern and southern unrecognized subspecies.
<i>Calystegia atriplicifolia</i> ssp. <i>burentis</i>	Richard K. Brummitt TM	Uncertain distribution, abundance, and circumscription from ssp. <i>atrichifolia</i> .
<i>Calystegia malacophylla</i> var. <i>berryi</i>	Richard K. Brummitt TM	Uncertain distinctiveness from ssp. <i>malacophylla</i> .
<i>Camissonia lewisi</i>	Warren L. Wagner TM /Peter H. Raven	Uncertain distribution, abundance, and circumscription of species in <i>C. lewisi</i> complex.
<i>Castilleja gleasonii</i>	T. I. Chuang [†] & Lawrence R. Heckard ^{† TM} /Orlando Mistretta/Margriet Wetherwax	<i>C. pruinosa</i> complex is highly variable and confusing.
<i>Castilleja monilena</i>	T. I. Chuang [†] & Lawrence R. Heckard ^{† TM} /Margriet Wetherwax	Is taxon true breeding and valid, or merely a sporadic F1 hybrid?
<i>Castilleja uliginosa</i>	T. I. Chuang [†] & Lawrence R. Heckard ^{† TM} /Margriet Wetherwax	Uncertain distinctiveness from <i>C. miniata</i> ssp. <i>minima</i> , but plant presumed extinct.
<i>Ceanothus confusus</i>	Clifford L. Schmidt TM	Possibly a variety of <i>C. prostratus</i> .
<i>Ceanothus divergens</i>	Clifford L. Schmidt TM	Possibly a variety of <i>C. purpureus</i> .
<i>Ceanothus masonii</i>	Clifford L. Schmidt TM /V. Thomas Parker	Possibly a variety of <i>C. gloriosus</i> .
<i>Ceanothus xotayensis</i>	Clifford L. Schmidt TM /Andrew C. Sanders	Is taxon true breeding and valid?
<i>Ceanothus sonomensis</i>	Clifford L. Schmidt TM	Possibly a variety of <i>C. cuneatus</i> .
<i>Chorizanthe cuspidata</i> vars. <i>cuspida</i> and <i>villosa</i>	James C. Hickman ^{† TM} /James L. Reveal & Clare Hardham	Uncertain circumscription of varieties; entire <i>Pungentes</i> complex needs study.
<i>Chorizanthe pungens</i> vars. <i>hartwegiana</i> and <i>pungens</i>	James C. Hickman ^{† TM} /James L. Reveal & Clare Hardham/R. Morgan/Barbara J. Ertter	Uncertain circumscription of varieties; entire <i>Pungentes</i> complex needs study.
<i>Chorizanthe robusta</i> vars. <i>hartwegiana</i> and <i>robusta</i>	James C. Hickman ^{† TM} /James L. Reveal & Clare Hardham/R. Morgan/Barbara J. Ertter	Uncertain circumscription of varieties; entire <i>Pungentes</i> complex needs study.

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Cirsium occidentale</i> var. <i>com-pactum</i>	David J. Keil & Charles E. Turner TM /Vernal L. Yadon	Uncertain circumscription of varieties; are differences environmentally induced?
<i>Clarkia mosquinii</i> spp. <i>mosqui-nii</i> and <i>xerophila</i>	Harlan Lewis TM /Lawrence Janeway/Les Gottlieb	Uncertain distribution, abundance, and distinctiveness of subspecies (are leaf differences environmentally induced?).
<i>Claytonia lanceolata</i> var. <i>peirsonii</i>	Kenton L. Chambers TM /John Miller/Orlando Mistretta	Uncertain distinctiveness from other varieties.
<i>Cordylanthus tenuis</i> ssp. <i>pallidens</i>	T. I. Chuang† & Lawrence R. Heckard† TM / Don Burk/Margriet Wetherwax	Uncertain distinctiveness from ssp. <i>viscidus</i> .
<i>Corethrodryne flaginifolia</i> vars. <i>incana</i> and <i>linifolia</i>	Meredith A. Lane TM	Uncertain circumscription from <i>Lessingia filaginifolia</i> var. <i>flaginifolia</i> , into which these rare varieties with unclear morphological basis and distribution have been merged.
<i>Corethrodryne leucophylla</i>	Meredith A. Lane TM	Uncertain circumscription from <i>Lessingia filaginifolia</i> var. <i>flaginifolia</i> , into which this taxon has been merged.
<i>Cryptantha clevelandii</i> var. <i>dissita</i>	Walter A. Kelly & Dieter H. Wilken TM	Uncertain distinctiveness from var. <i>clevelandii</i> .
<i>Cryptantha ratianii</i>	Walter A. Kelly & Dieter H. Wilken TM	Uncertain distinctiveness from <i>C. decipiens</i> .
<i>Cryptantha scoparia</i>	Walter A. Kelly & Dieter H. Wilken TM	Uncertain distinctiveness from <i>C. nevadensis</i> .
<i>Cupressus stephensonii</i>	Jim A. Bartel TM /Connie Millar	Uncertain distinctiveness from <i>C. arizonica</i> ssp. <i>arizonica</i> .
<i>Delphinium luteum</i>	Michael J. Warnock TM	Uncertain extent of introgression with close relatives.
<i>Delphinium variegatum</i> spp. <i>kinkense</i> and <i>thornei</i>	Michael J. Warnock TM	Uncertain distinctiveness of subspecies.
<i>Dendromecon harfordii</i> vars. <i>harfordii</i> and <i>rhamnoides</i>	Curtis Clark TM	Highly variable; uncertain distinctiveness of varieties.
<i>Dicentra formosa</i> ssp. <i>oregana</i>	Curtis Clark TM /Kingsley Stern	Uncertain distinctiveness from ssp. <i>formosa</i> .
<i>Dichanthelium lanuginosum</i> var. <i>thermale</i>	Robert Webster TM /Sally deBecker	Uncertain circumscription from <i>Panicum acuminatum</i> var. <i>acuminatum</i> .

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Dudleya alatae</i>	Jim A. Bartel ^{JM} /Craig Reiser/James C. Dice/ Kei Nakai/Reid Moran	Uncertain distinctiveness from <i>D. saxosa</i> ssp. <i>aloides</i> .
<i>Echinocereus engelmannii</i> var. <i>howei</i>	Edward F. Anderson ^{JM} /Maile Neel/Lyman Benson†	Uncertain distinctiveness of this and other varieties.
<i>Emperium nigrum</i> ssp. <i>herma-</i> <i>phroidium</i>	Fosieé Tahbaz ^{JM}	Uncertain validity of subspecies; if valid, are any CA plants this variety?
<i>Eremalche kernensis</i>	David M. Bates ^{JM} /Dean W. Taylor & W. B. Davilla/Susan Mazer	Uncertain circumscription of taxa in the <i>E. parryi/E. ker-</i> <i>nensis</i> complex.
<i>Erigeron calvus</i>	Guy L. Nesom ^{JM}	Unknown distribution, abundance, and distinctiveness from <i>E. divergens</i> and <i>E. aphanactis</i> var. <i>aphanactis</i> .
<i>Eriogonum beatleyae</i>	James C. Hickman† ^{JM} /James L. Reveal	Uncertain distinctiveness from <i>E. ochrocephalum</i> and <i>E.</i> <i>rosense</i> .
<i>Eriogonum eastwoodianum</i>	James C. Hickman† ^{JM} /James L. Reveal	Uncertain distinctiveness from <i>E. temblorense</i> and <i>E.</i> <i>vestitum</i> .
<i>Eriogonum luteolum</i> var. <i>cani-</i> <i>num</i>	James C. Hickman† ^{JM} /James L. Reveal	Uncertain circumscription from var. <i>luteolum</i> ; distribu- tion needs clarification.
<i>Eriogonum temblorense</i>	James C. Hickman† ^{JM} /James L. Reveal	Uncertain distinctiveness from <i>E. eastwoodianum</i> and <i>E.</i> <i>vestitum</i> .
<i>Eriogonum vestitum</i>	James C. Hickman† ^{JM} /James L. Reveal	Uncertain distinctiveness from <i>E. eastwoodianum</i> and <i>E.</i> <i>temblorense</i> .
<i>Eryngium spinosepalum</i>	Lincoln Constance ^{JM}	Uncertain degree of introgression with <i>E. castrense</i> and <i>E. vaseyi</i> .
<i>Erythromium howellii</i>	Geraldine A. Allen ^{JM} /James R. Shevock	Uncertain distinctiveness from <i>E. citrinum</i> .
<i>Eschscholzia minutiflora</i> ssp. <i>twisselmannii</i>	Curtis Clark ^{JM} /Mark Faull	Uncertain distinctiveness of subspecies.
<i>Eschscholzia procera</i>	Curtis Clark ^{JM}	Uncertain distinctiveness from <i>E. californica</i> .
<i>Fritillaria roderickii</i>	Bryan D. Ness ^{JM} /Walter Knight	Uncertain distinctiveness from <i>F. biflora</i> var. <i>biflora</i> .
<i>Genista affinis</i> var. <i>parviflora</i>	James S. Pringle ^{JM}	Unknown distribution (is plant in CA?); abundance, and distinctiveness from var. <i>ovata</i> .
<i>Helianthemum suffrutescens</i>	Elizabeth McClintock ^{JM} /John Willoughby and James R. Shevock	Uncertain distinctiveness from <i>H. scoparium</i> .

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Helianthus exilis</i>	David J. Keil ^{IM} /S. K. Jain & A. M. Olivieri	Uncertain distinctiveness from <i>H. bolanderi</i> .
<i>Hemizonia congesta</i> ssp. <i>leuccephala</i>	David J. Keil ^{IM} /Barry Tanowitz/Bruce G. Baldwin	Uncertain distinctiveness from ssp. <i>congesta</i> ; herbarium specimens may be indistinguishable.
<i>Heuchera duranii</i>	Patrick E. Elvander ^{IM}	Uncertain distinctiveness from <i>H. parvifolia</i> .
<i>Horkelia cuneata</i> ssp. <i>sericea</i> and <i>puberula</i>	Barbara J. Eritter ^{IM}	Complex clinal variation of subspecies.
<i>Horkelia marinensis</i>	Barbara J. Eritter ^{IM}	Are Mendocino Co. populations near Ft. Bragg varietally distinct?
<i>Ivesia argyrocoma</i>	Barbara J. Eritter ^{IM}	Are Baja California populations varietally distinct?
<i>Lathyrus sulphureus</i> var. <i>argillaceus</i>	Duane Isely ^{IM} /Steven Broich	Uncertain distinctiveness from var. <i>sulphureus</i> ; distribution and abundance poorly known.
<i>Lavatera assurgentiflora</i> spp. <i>assurgentiflora</i> and <i>glabra</i>	Steven R. Hill ^{IM} /R. N. Philbrick/Marty Ray	Uncertain distinctiveness of subspecies.
<i>Lessingia arachnoidea</i>	Meredith A. Lane ^{IM}	Uncertain species circumscription; relationship to <i>L. hololeuca</i> unclear.
<i>Lewisia cotyledon</i> vars. <i>heckneri</i> and <i>howellii</i>	Lauramay T. Dempster ^{IM}	Uncertain distinctiveness of rare varieties.
<i>Lewisia oppositifolia</i>	Lauramay T. Dempster ^{IM}	CA plants possibly hybrids with <i>C. nevadensis</i> .
<i>Lewisia serrata</i>	Lauramay T. Dempster ^{IM} /Lawrence R. Heckard [†] & G. L. Siebbs	Uncertain distinctiveness from <i>L. canescens</i> .
<i>Limnanthes floccosa</i> ssp. <i>bellingeriana</i>	Robert Ornduff ^{IM} /Mary T. Kalin Arroyo/Darlene Southworth/Lincoln Constance ^{IM}	Uncertain distinctiveness in CA from ssp. <i>floccosa</i> .
<i>Lomatium foeniculaceum</i> ssp. <i>inyoense</i>	Teresa Sholars ^{IM} /Vernal L. Yadon	Possibly a form induced by high-altitude conditions.
<i>Lupinus albifrons</i> var. <i>abramsi</i>		Uncertain distribution and distinctiveness from var. <i>albifrons</i> ; only specimens from the Partington Ridge area, Monterey Co. match the type.
<i>Lupinus croceus</i> var. <i>pilosellus</i>	Teresa Sholars ^{IM}	Uncertain distinctiveness from var. <i>croceus</i> .
<i>Lupinus elatus</i>	Teresa Sholars ^{IM}	Unclear basis of distinction from <i>L. adsurgens</i> and <i>L. andersonii</i> .

TABLE I. CONTINUED

Scientific name	Authorities	Research problem
<i>Lupinus eximius</i>	Teresa Sholars TM	Uncertain distinctiveness from <i>L. arboreus</i> ; taxonomic confirmation needed for Sonoma Co. plants.
<i>Lupinus magnificus</i> vars. <i>glarecola</i> and <i>hesperius</i>	Teresa Sholars TM	Uncertain distinctiveness of rare varieties.
<i>Lupinus milt-bakeri</i>	Rhonda Riggins TM /Teresa Sholars/Walter Knight	Uncertain distinctiveness from <i>L. luteolus</i> .
<i>Lycium brevipes</i> var. <i>hassei</i>	Michael Nee TM /Andrew C. Sanders	Uncertain distinctiveness from var. <i>brevipes</i> .
<i>Lycium verrucosum</i>	Michael Nee TM	Possibly a form of <i>L. brevipes</i> .
<i>Malacothamnus acutatus</i>	David M. Bates TM	Uncertain distinctiveness from <i>M. fasciculatus</i> .
<i>Malacothamnus davidsonii</i>	David M. Bates TM	Unclear distribution and basis of distinction from <i>M. fasciculatus</i> .
<i>Malacothamnus fasciculatus</i> var. <i>nesioticus</i>	David M. Bates TM /Susan M. Swensen et al.*	Uncertain distinctiveness from other varieties.
<i>Malacothamnus gracilis</i>	David M. Bates TM	Uncertain distinctiveness from <i>M. jonesii</i> .
<i>Malacothamnus hallii</i>	David M. Bates TM	Uncertain distinctiveness from <i>M. fasciculatus</i> .
<i>Malacothamnus helleri</i>	David M. Bates TM	Uncertain distinctiveness from <i>M. fremontii</i> .
<i>Malacothamnus mendocinensis</i>	David M. Bates TM	Uncertain distinctiveness from <i>M. fasciculatus</i> .
<i>Malacothamnus niveus</i>	David M. Bates TM	Uncertain distinctiveness from <i>M. jonesii</i> .
<i>Malacothamnus palmeri</i> vars. <i>invulnerans</i> , <i>lucitanus</i> , and <i>palmeri</i>	David M. Bates TM /Vernal L. Yadon	Uncertain distinctiveness of varieties.
<i>Malacothamnus parishii</i>	David M. Bates TM	Uncertain distinctiveness from <i>M. fasciculatus</i> .
<i>Mimulus acutidens</i>	David M. Thompson TM	Uncertain distribution, abundance, and distinctiveness from <i>M. inconspicuus</i> .
<i>Mimulus aridus</i>	David M. Thompson TM	Uncertain circumscription of this and related taxa.
<i>Mimulus brachiatus</i>	David M. Thompson TM	Uncertain distribution and distinctiveness from <i>M. layneae</i> .
<i>Mimulus brandegeei</i>	David M. Thompson TM	Uncertain distinctiveness from <i>M. latifolius</i> , but presumed extinct.
<i>Mimulus diffusus</i>	David M. Thompson TM	Uncertain distinctiveness from <i>M. palmeri</i> .

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Mimulus flemingii</i>	David M. Thompson TM	Uncertain circumscription of this and related taxa.
<i>Mimulus glabratus</i> ssp. <i>utahensis</i>	David M. Thompson TM	Uncertain distinctiveness from <i>M. guttatus</i> .
<i>Mimulus grayi</i>	David M. Thompson TM	Uncertain distinctiveness from <i>M. inconspicuus</i> .
<i>Mimulus microphyllus</i>	David M. Thompson TM	Uncertain distinctiveness from <i>M. guttatus</i> .
<i>Mimulus ratianni</i> ssp. <i>decurvatus</i>	David M. Thompson TM	Uncertain distinctiveness from ssp. <i>ratianni</i> .
<i>Mimulus subsecundus</i>	David M. Thompson TM	Uncertain distinctiveness from <i>M. fremontii</i> .
<i>Mimulus whipplei</i>	David M. Thompson TM	Uncertain distinctiveness from <i>M. guttatus</i> .
<i>Monardella Antonia</i> ssp. <i>antonina</i> and <i>benitensis</i>	James D. Jokers TM /Clare Hardham	Uncertain circumscription and distribution of varieties, which are similar to <i>M. villosa</i> ssp. <i>villosa</i> .
<i>Monardella linoides</i> ssp. <i>oblonga</i>	James D. Jokers TM	Uncertain distinctiveness from ssp. <i>linoides</i> .
<i>Monardella robisonii</i>	James D. Jokers TM	Possibly a variety of <i>M. linoides</i> ; taxonomic confusion contributes to uncertain distribution in California; may occur in Baja California.
<i>Myosurus minimus</i> ssp. <i>apus</i>	Dieter H. Wilken TM /Alan Whittmore	Uncertain distribution and distinctiveness from <i>M. sessilis</i> , possibly a poorly stabilized hybrid between <i>M. minimus</i> and <i>M. sessilis</i> , at least in the Central Valley.
<i>Opuntia munizii</i>	Bruce D. Parfitt & Marc A. Baker TM /Andrew C. Sanders	Origin uncertain but taxon is valid; possible hybrid of <i>O. bigelovii</i> and <i>O. echinocarpa</i> .
<i>Opuntia parryi</i> var. <i>serpentina</i>	Bruce D. Parfitt & Marc A. Baker TM /Lyman Benson [†]	Uncertain circumscription from var. <i>parryi</i> .
<i>Opuntia wigginsii</i>	Bruce D. Parfitt & Marc A. Baker TM	Uncertain distinctiveness from <i>O. ramosissima</i> ; possibly a sporadic hybrid between <i>O. ramosissima</i> and <i>O. echinocarpa</i> .
<i>Pedicularis dudleyi</i>	Linda Ann Vorobik TM	Southern plants somewhat distinctive; variation in the species needs further study.
<i>Penstemon cinereus</i>	Noel H. Holmgren TM /Elizabeth Chase Neese	Uncertain distinctiveness from <i>P. humilis</i> var. <i>humilis</i> .
<i>Perideridia lepiocarpa</i>	Lincoln Constance TM	Uncertain distinctiveness from <i>P. oregana</i> .
<i>Petalonyx Thurberi</i> ssp. <i>gilmanii</i>	Barry A. Prigge TM	Uncertain distinctiveness from ssp. <i>thurberi</i> .
<i>Phacelia amabilis</i>	Dieter H. Wilken, Richard R. Halse & Robert W. Patterson TM /Lincoln Constance	Uncertain distinctiveness from <i>P. crenulata</i> .

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Phacelia ciliata</i> var. <i>opaca</i>	Dieter H. Wilken, Richard R. Halse & Robert W. Patterson TM /Lincoln Constance	Uncertain distinctiveness from var. <i>ciliata</i> .
<i>Plagiobothrys chorisianus</i> var. <i>chorisianus</i>	Timothy C. Messick ^{JM}	Uncertain distinctiveness from var. <i>hickmani</i> ; differences may be environmentally induced.
<i>Plagiobothrys diffusus</i>	Timothy C. Messick ^{JM} /Roy E. Buck	Uncertain distribution and distinctiveness from <i>P. reticulatus</i> var. <i>rossianorum</i> .
<i>Plagiobothrys glaber</i>	Timothy C. Messick ^{JM}	Possibly a variety of <i>P. stipitatus</i> .
<i>Plagiobothrys glypticarpus</i> var. <i>modestus</i>	Timothy C. Messick ^{JM}	Uncertain position in the <i>P. glypticarpus</i> / <i>P. distantiiflorus</i> complex; possibly a minor variant or hybrid.
<i>Plagiobothrys myosotoides</i>	Timothy C. Messick ^{JM}	Identification uncertain; unclear relationship to <i>P. torreyi</i> complex. More South American specimens needed for comparison with CA material.
<i>Platystemon californicus</i> var. <i>ciliatus</i>	Curtis Clark ^{JM} /R. N. Philbrick/Gary Hannan	Uncertain distinctiveness from var. <i>californicus</i> .
<i>Pogogyne douglasii</i> ssp. <i>parviflora</i>	James D. Jokers ^{JM}	Uncertain distinctiveness of subspecies; Central Valley populations of ssp. <i>parviflora</i> possibly distinct from those of the Coast Ranges.
<i>Polemonium chartaceum</i>	Dieter H. Wilken ^{JM} /Daniel Pritchett*	Disjunct occurrences may be taxonomically distinct.
<i>Polygonum marinense</i>	James C. Hickman† ^{JM}	Uncertain distinctiveness; related to <i>P. aviculare</i> , possibly = <i>P. robertii</i> (in <i>The Jepson Manual</i>), not native in CA.
<i>Polygonum polycaloides</i> ssp. <i>esotericum</i>	James C. Hickman† ^{JM} /Glen Clifton	Uncertain circumscription of <i>P. polycaloides</i> subspecies.
<i>Psilocarphus elatior</i>	James D. Morefield ^{JM}	Uncertain distribution and abundance in northern CA; possibly a variant of <i>P. brevisissimus</i> var. <i>brevisissimus</i> .
<i>Puccinellia californica</i>	Jerrold I. Davis ^{JM} /Andrew C. Sanders	Uncertain distinctiveness from <i>Puccinellia simplex</i> .
<i>Puccinellia parishii</i>	Jerrold I. Davis ^{JM}	Uncertain circumscription from <i>Torreya</i> <i>ochroba pallida</i> var. <i>paciiflora</i> .
<i>Rhus trilobata</i> var. <i>simplicifolia</i>	Dieter H. Wilken ^{JM} /Geoffrey A. Levin	Uncertain distribution and distinctiveness of varieties.
<i>Ribes amarum</i> var. <i>hoffmannii</i>	Michael R. Mesler & John O. Sawyer, Jr. ^{JM}	Uncertain distinctiveness from var. <i>amarum</i> .
<i>Ribes menziesii</i> var. <i>ioxoderme</i>	Michael R. Mesler & John O. Sawyer, Jr. ^{JM}	Uncertain distinctiveness of varieties.

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Rubus glaucifolius</i> var. <i>gandei</i>	Barbara J. Ertter TM	Uncertain distinctiveness from var. <i>glaucifolius</i> .
<i>Salvia dorrii</i> var. <i>incana</i>	Deborah Engle Averett & Kurt R. Neises TM /Jeffrey L. Strachan	Uncertain distinctiveness of variety in CA.
<i>Sanguisorba officinalis</i>	Barbara J. Ertter TM /Calder & Roy Taylor	CA plants may be ssp. <i>microcephala</i> .
<i>Scrophularia atrata</i>	Margriet Wetherwax TM /David Magnay	Uncertain degree of introgression with <i>S. californica</i> ssp. <i>floribunda</i> .
<i>Sedum laxum</i> spp. <i>flavidum</i> and <i>heckneri</i>	Melinda F. Denton† TM	Uncertain distinctiveness of rare subspecies.
<i>Senecio clevelandii</i> vars. <i>cleve-</i> <i>landii</i> and <i>heterophyllus</i>	Theodore M. Barkley TM	Uncertain distinctiveness of varieties.
<i>Silene occidentalis</i> ssp. <i>longistip-</i> <i>itata</i>	Dieter H. Wilken TM /John K. Morton	Uncertain distribution and distinctiveness from ssp. <i>occi-</i> <i>dentalis</i> .
<i>Solanum elaeagnifolium</i>	Michael Nee TM /Tim Ross/Steve Junak	Uncertain circumscription from <i>S. wallacei</i> . <i>S. xanti</i> complex needs revision.
<i>Solanum wallacei</i>	Michael Nee TM /Tim Ross/Steve Junak	Uncertain distribution and circumscription from <i>S. cloke-</i> <i>yi</i> and <i>S. xanti</i> ; mainland occurrences in Santa Barbara and San Luis Obispo counties are probably <i>S. xanti</i> . <i>S. xanti</i> complex needs revision.
<i>Streptanthus albidus</i> ssp. <i>per-</i> <i>moenus</i>	Roy E. Buck, Dean W. Taylor & Arthur R. Kruckeberg TM /Niall F. McCarten	Uncertain distribution and distinctiveness from <i>S. gan-</i> <i>dulosus</i> .
<i>Streptanthus batrachopus</i>	Roy E. Buck, Dean W. Taylor & Arthur R. Kruckeberg TM	Uncertain distinctiveness from north coast plants, which may be an undescribed taxon.
<i>Streptanthus glandulosus</i> var. <i>hoffmannii</i>	Roy E. Buck, Dean W. Taylor & Arthur R. Kruckeberg TM /Roger Raiche	Uncertain circumscription from ssp. <i>secundus</i> .
<i>Streptanthus glandulosus</i> var. <i>sonomensis</i>	Roy E. Buck, Dean W. Taylor & Arthur R. Kruckeberg TM /Roger Raiche	Uncertain circumscription from ssp. <i>secundus</i> .
<i>Streptanthus morrisonii</i> spp. <i>elatus</i> , <i>hiriflorus</i> , <i>kruckebergii</i> , and <i>morrisonii</i>	Roy E. Buck, Dean W. Taylor & Arthur R. Kruckeberg TM /Rebecca Dolan & Lawrence F. LaPré/Roger Raiche	Uncertain circumscription of varieties.

TABLE 1. CONTINUED

Scientific name	Authorities	Research problem
<i>Tiarella trifoliata</i> var. <i>trifoliata</i>	Patrick E. Elvander ^{IM} /Patricia K. Holmgren	Uncertain distribution and distinctiveness from var. <i>unifolia</i> .
<i>Trichocoronis wrightii</i> var. <i>wrightii</i>	A. Michael Powell ^{IM} /Andrew C. Sanders	Perhaps best treated as a full species distinct from Texas plants.
<i>Trifolium polyodon</i>	Duane Isely ^{IM} /Vernal L. Yadon/John M. Gillett/Michael Vincent	Uncertain distinctiveness from <i>T. variegatum</i> .
<i>Trifolium trichocalyx</i>	Duane Isely ^{IM} /Vernal L. Yadon/John M. Gillett/Michael Vincent	Possible unstabilized hybrid.
<i>Vaccinium coccineum</i>	Gary D. Wallace ^{IM} /Jim Pushnik	Uncertain distinctiveness from <i>V. membranaceum</i> .

own or their students' research efforts, and to contribute information in their possession to resolve these issues. In addition to a vast and complex flora replete with rare plants, California has a remarkably large and active botanical community. These factors converge to make it most difficult for any single party to have a comprehensive understanding of what rare plant research is required and who is doing it. We propose that this function be assumed by the CNPS Rare Plant Scientific Advisory Committee (RPSAC), which already maintains active databases tracking progress on rare plant information needs in California. Such a system will serve several functions, including minimizing duplication of effort and focusing research on issues of scientific and conservation importance. In particular, students who are embarking on research programs at levels ranging from senior theses to doctoral dissertations may find topics of interest, or may be able to restructure current studies to contribute information of conservation importance.

This effort integrates well with a new CNPS grant program. Starting in 1995, the RPSAC will administer modest grants of up to \$1000/year to encourage resolution of taxonomic and distributional uncertainty which limits protection of California's rare flora. Information on this grant program will soon be published in the CNPS *Bulletin*, and is also available from the CNPS State Office, Rare Plant Program, or Vice President for Plant Programs.¹ Comparable grants are also available from the Hardman Foundation and, to a limited extent, from the CNPS Grants Committee.

Note that we have included only scant outlines of each problem in the tables; readers will need to consult existing published references such as Munz and Keck (1973), Munz (1974), the *Inventory*, the *Manual*, and other treatments and references for a more detailed understanding. In most cases the CNPS Rare Plant Program and the NDBB have additional information on file or in digital form for distribution. We hope that persons planning research programs will contact the authorities listed in the tables to discern current research efforts and help guide their own. We also recommend consulting with *Flora of North America* (FNA) authors for more information, since many treatments of California plants are currently in preparation and hopefully some of the taxonomic and distributional enigmas listed here will be clarified by FNA treatments. (Contact the Missouri Botanical Garden in St. Louis for FNA author information; we have included authors known to us.)

The present compilation is far from complete, and we welcome additional information to reduce gaps in our knowledge of what

¹ CNPS State Office phone number is (916) 447-2677, Rare Plant Program is (916) 324-3816 or 327-0714, and Vice President for Plant Programs is (415) 705-2691.

needs to be done. Furthermore, we emphasize that our intention here is not to offend conscientious workers who may have settled these issues already, or feel that they have. We acknowledge our ignorance of much important work on California's rare plants, so please send us your important conclusions if it appears we are unfamiliar with them. For example, although published several years ago, we only recently became aware of a taxonomic treatment affirming that *Scutellaria holmgreniorum* is a synonym of *S. nana* (Olmstead 1990); we can now evaluate this work and consider deleting *S. holmgreniorum* from the *Inventory* and NDDB *Special Plants List* (NDDB 1994).

Publication of results in peer reviewed scientific journals promotes acceptance of taxonomic ideas, and generally, unpublished conclusions must be regarded as tentative. In several cases compiled here, research having important bearing on California plant conservation has been completed but not yet published, as with current studies of coastal *Arabis* (Vorobik 1994, personal communication). These cases are identified in the tables for the sake of completeness. The remaining plants in Tables 1 and 3 are included either because information is lacking (the vast majority) or we judge that no adequate taxonomic treatments exist.

RESEARCH NEEDS

Endangered species protection rests on widespread agreement about a species' taxonomic status, distribution and abundance, and type and magnitude of threats. Uncertainty in any of these areas encourages opponents of protection, who frequently will claim that a taxon is not worthy of recognition or should be recognized at some lower taxonomic level, is more common than biologists think, or is not severely threatened. Some examples are given below in the text. Unlike Messick (1987), who addressed a broad range of necessary studies in his useful compendium of research needs for California rare plants, here we stress only the distributional and taxonomic information necessary to better assign conservation status and prioritize protection activities, which may include more detailed future autecological, genetic, and recovery research.

TAXONOMIC UNCERTAINTY

Uncertainty regarding the nomenclatural status of rare species (Table 1) lowers their protection priority, and typically must be resolved before protection or conservation measures can be established. In 1990, a petition was filed with the State of California to list *Chorizanthe robusta* var. *hartwegii* as an endangered taxon. The petition was challenged by listing opponents and their biological

consultant on the grounds that the var. *hartwegii* is indistinct from var. *robusta*. An inconclusive battle of taxonomic experts ensued, and the petition was subsequently rejected at the State level, primarily because of taxonomic uncertainty. Convinced that taxonomic controversy would complicate Federal listing of this plant and three of its close relatives, the US Fish and Wildlife Service convened a panel of experts from UC Berkeley to review the distribution and taxonomy of the *Chorizanthe pungens/C. robusta* complex. The panel returned the verdict that the complex does have recognizable and modally well-defined phases without strong boundaries (Ertter 1990). The Service proceeded with the listings, though it sidestepped the taxonomic issues in part by listing *C. robusta* as a whole rather than listing the two varieties separately, an option because the entire species is endangered. Nevertheless, taxonomic uncertainty caused delays that were costly to conservationists since time was wasted and protection lagged, and expensive to opponents who squandered money on biological consultants and lawyers hired to challenge the authenticity of taxa. And had the outcome been different and the taxa judged indistinct, once again conservationists would have needlessly sacrificed credibility by investing time and effort to protect taxa of dubious taxonomic validity.

The rough criteria that we established for inclusion on the list of taxonomically unresolved rare California plants are outlined below and in the next paragraph. Many of the plants included here were reduced to synonymy or embedded within other entries in the *Manual*, yet for various reasons may merit taxonomic recognition (Skinner and Ertter 1993, Skinner and Pavlik 1994). For example, the taxonomic status of *Dudleya alainae* remains controversial despite its designation as a synonym of *D. aloides* ssp. *saxosa* in the *Manual*. Other taxa included here were recognized or mentioned in the *Manual*, but authors expressed uncertainty about the proper level of taxonomic recognition or were unsure of taxonomic limits. For example, knowledgeable field botanists in Sonoma County feel that the subspecies of *Streptanthus morrisonii* are distinct and merit separate recognition, notwithstanding the parenthetical (embedded) treatment of those subspecies in the *Manual* and ongoing confusion regarding their circumscription.

Taxa at the specific, subspecific, or varietal rank that are known to introgress with close relatives, or that hybridize sporadically but which nevertheless are morphologically or genetically defined over their core distribution are not included here. Many rare plants in *Arctostaphylos*, *Chorizanthe*, *Eriogonum*, *Monardella*, and many genera of Asteraceae, to name only a very few, display this pattern. In fact, this phenomenon has informally been referred to as the "California pattern" since it is so widespread here. Among other causes, it arises from the relative modernity of much of our flora

and resultant incomplete development of reproductive isolating mechanisms (Stebbins and Major 1965). It follows that the existence of hybridization or zones of introgression between otherwise well-defined taxa does not invalidate them, nor in most cases would additional study clarify the situation. Taxa are included below if there is significant uncertainty about the degree of introgression, and consequently, about the distributions of taxa involved. In theory, conservationists might want to minimize awareness of the extent of hybridization between rare plants for at least two reasons: typically there is no legal protection for hybrids, and the existence of hybrids or broad zones of intergradation is often interpreted by non-biologists as evidence that taxa are not distinct. The reality of Nature is much less convenient.

The distribution of taxonomic problems affecting rare plants as currently catalogued in the *Inventory* is highly uneven across different groups (Table 2). Some large genera typically considered to be taxonomically or distributionally complex are riddled with taxonomic problems affecting rare representatives (e.g., *Lupinus*, *Mimulus*, *Streptanthus*, *Chorizanthe*, *Malacothamnus*), while, by our accounting, others (e.g., *Astragalus*, *Arctostaphylos*, *Galium*, *Dudleya*, *Calochortus*, and *Carex*) are virtually free of such problems. A simple explanation of this inconsistency is not forthcoming. The history of taxonomic study probably plays a major role in any explanation, however, since some groups have been treated more frequently, more recently, or more comprehensively, leading either to cleaner taxonomic schemes or to the perception that they are cleaner (Shevock 1993). In other cases, lack of taxonomic uncertainty in a genus indicates lack of intensive research; until studied some genera seemingly present few problems. Regardless, competent specialists who can provide clean identifications contribute to perception that groups are taxonomically tractable.

Evolutionary history also probably contributes significantly, since some groups apparently do consist of specific and infraspecific taxa that are better demarcated and hence more easily separable. It is also likely that in some difficult groups such as *Arctostaphylos* or *Dudleya*, messy distributional patterns and resulting taxonomies are acknowledged and accepted by the botanical public and not considered to be problematic. With respect to any patterns or lack thereof in Table 2, it is probably safest merely to reiterate that Table 1—the basis of Table 2—is an incomplete compendium of rare plant taxonomic problems in California that is based on our current knowledge. We are not suggesting that genera missing or poorly represented in Table 2 are necessarily taxonomically clean; we merely assert our current ignorance of taxonomic controversies that affect our ability to define and protect rare representatives in these groups.

Many of the problems compiled in Table 1 can be approached

TABLE 2. TAXONOMIC UNCERTAINTY AMONG CALIFORNIA GENERA WITH MANY RARE PLANTS. Taxa are arranged by descending representation in the *Inventory*. Column 3 (number of *Inventory* taxa with taxonomic problems) sums the problematic taxa from Table 1.

Genus	No. taxa in <i>Inventory</i>	No. <i>Inventory</i> taxa w/ tax. problems	% w/tax. problems
<i>Eriogonum</i>	71	5	7
<i>Astragalus</i>	66	0	0
<i>Arctostaphylos</i>	57	1	2
<i>Lupinus</i>	30	7	23
<i>Galium</i>	29	0	0
<i>Mimulus</i>	29	12	41
<i>Phacelia</i>	28	2	7
<i>Dudleya</i>	27	1	4
<i>Calochortus</i>	25	0	0
<i>Carex</i>	25	0	0
<i>Clarkia</i>	25	2	8
<i>Arabis</i>	24	3	13
<i>Streptanthus</i>	24	8	33
<i>Chorizanthe</i>	23	6	26
<i>Erigeron</i>	23	1	4
<i>Monardella</i>	23	4	17
<i>Delphinium</i>	19	2	11
<i>Ceanothus</i>	18	5	28
<i>Penstemon</i>	18	1	6
<i>Allium</i>	17	0	0
<i>Castilleja</i>	17	3	18
<i>Cordylanthus</i>	17	1	6
<i>Ivesia</i>	17	0	0
<i>Lomatium</i>	16	1	6
<i>Malacothamnus</i>	16	12	75
<i>Sidalcea</i>	16	0	0
<i>Cryptantha</i>	15	3	20
<i>Navarretia</i>	15	0	0
<i>Draba</i>	14	0	0
<i>Hemizonia</i>	14	1	7
<i>Linanthus</i>	14	0	0
<i>Fritillaria</i>	13	1	8
<i>Horkelia</i>	13	3	23
<i>Lotus</i>	13	0	0
<i>Atriplex</i>	12	1	8
<i>Lilium</i>	12	0	0
<i>Plagiobothrys</i>	12	5	42
<i>Ribes</i>	12	2	17
<i>Camissonia</i>	11	1	9
<i>Cirsium</i>	11	1	9
<i>Senecio</i>	11	2	18
<i>Erysimum</i>	10	0	0
<i>Juncus</i>	10	0	0
<i>Lewisia</i>	10	4	40
<i>Calystegia</i>	9	2	22
<i>Cupressus</i>	9	1	11
<i>Erythronium</i>	9	1	11

TABLE 2. CONTINUED

Genus	No. taxa in Inventory	No. Inventory taxa w/ tax. problems	% w/tax. problems
<i>Heuchera</i>	9	1	11
<i>Opuntia</i>	9	3	33
<i>Potentilla</i>	9	0	0
<i>Trifolium</i>	9	2	22
<i>Eriophyllum</i>	8	0	0
<i>Hesperolinon</i>	8	0	0
<i>Lessingia</i>	8	1	13
<i>Sedum</i>	8	2	25
<i>Epilobium</i>	7	0	0
<i>Gilia</i>	7	0	0
<i>Hulsea</i>	7	0	0
<i>Lathyrus</i>	7	1	14
<i>Layia</i>	7	0	0
<i>Limnanthes</i>	7	1	14
<i>Arnica</i>	6	1	17
<i>Botrychium</i>	6	0	0
<i>Brodiaea</i>	6	0	0
<i>Campanula</i>	6	0	0
<i>Eryngium</i>	6	1	17
<i>Eschscholzia</i>	6	2	33
<i>Madia</i>	6	0	0
<i>Oxytheca</i>	6	0	0
<i>Pedicularis</i>	6	1	17
<i>Pinus</i>	6	0	0
<i>Poa</i>	6	0	0
<i>Potamogeton</i>	6	0	0
<i>Salvia</i>	6	1	17
<i>Silene</i>	6	1	17
<i>Viola</i>	6	0	0
<i>Acanthomintha</i>	5	0	0
<i>Eriastrum</i>	5	0	0
<i>Ericameria</i>	5	0	0
<i>Gentiana</i>	5	1	20
<i>Iris</i>	5	0	0
<i>Lepidium</i>	5	0	0
<i>Malacothrix</i>	5	0	0
<i>Minuartia</i>	5	0	0
<i>Muhlenbergia</i>	5	0	0
<i>Orcuttia</i>	5	0	0
<i>Perideridia</i>	5	1	20
<i>Pogogyne</i>	5	1	20
<i>Sanicula</i>	5	0	0
<i>Selaginella</i>	5	0	0
<i>Thermopsis</i>	5	0	0
<i>Triteleia</i>	5	0	0

through standard systematic methodology involving review of existing herbarium specimens and literature, examination of type specimens, field surveys and specimen collecting to document distribution and ecology, and morphological comparisons, including relatively sophisticated statistical procedures such as multivariate analyses. Resolution of some taxonomic controversies will be facilitated by molecular studies of the focus taxon and its close relatives, or through a combination of morphological and molecular approaches. Recent comparison of allozymes and RAPD genomic markers allowed Swensen et al. (1995) to conclude that *Malacothamnus fasciculatus* var. *nesioticus*, which was reduced to synonymy in the *Manual*, merits taxonomic recognition. Common garden experiments, which minimize the effect of environment on phenotypic expression, can be most illuminating. Regardless of the approach, broad sampling covering the distribution of subject taxa and careful selection of close relatives to be included in any study is crucial. Barring explicit demonstrations of actual reproductive isolation, only with an understanding of the degree of variation typically present in taxa of a given rank for a given group can appropriate taxonomic decisions be made in that group.

DISTRIBUTIONAL UNCERTAINTY

The recent discoveries in California of outstanding botanical novelties such as *Neviusia cliftonii* (Shevock et al. 1992) and *Ceanothus ophiochilus* (Boyd et al. 1991) highlight the often substantial gaps in our knowledge of California's plants and where they occur (see also Shevock and Taylor 1987). Many areas of the state are poorly collected, and our knowledge of those floras is correspondingly weak. Very recent surveys by Glenn Clifton and other consulting biologists in the Modoc Plateau have revealed nine taxa previously unknown in California, including *Atriplex gardneri* var. *falcata*, *Psoralidium lanceolatum*, *Stanleya viridisflora*, and *Triteleia grandiflora* ssp. *howellii*. But poorly known areas need not be remote. During field work conducted over the past three years, one of the authors (A. Sanders) has added over 100 new plants to the flora of the San Bernardino Mts., a much botanized range that is easily visible from Los Angeles, the second largest metropolis in the United States.

Less spectacular than striking new discoveries such as *Neviusia* but no less important are gaps in our understanding of the distributions of other California plants known for some time to be rare or endangered. These taxa are often small (e.g., *Psilocarphus*), overlooked because of taxonomic bias (e.g., many pteridophytes), or difficult to identify because of the presence of sibling species (e.g., *Camissonia lewisii* complex) or extensive hybridization (e.g., *Arc-*

tostaphylos, *Calystegia*, *Corethrogynne filaginifolia* vars., *Delphinium*, or *Lupinus*). Others such as *Potamogeton* live in aquatic habitats that are rarely surveyed or collected by terrestrial botanists. Many of these plants are also overlooked since they flower infrequently and are usually encountered in the vegetative state.

Distributional uncertainty (Table 3) limits conservation action in several ways. Taxa thought to be absent from an area are not included on "potential lists" of plants to be looked for during the environmental disclosure phase prior to completion of development projects which are subject to environmental quality laws (e.g., the California Environmental Quality Act and the National Environmental Policy Act). Despite the requirement that such fieldwork be floristic in nature and not focus on high probability rarities (Department of Fish and Game 1984), the reality is often otherwise. If taxa are not looked for and hence not found, protection at these sites is clearly compromised. Equally important, without firm knowledge of distribution and abundance it is impossible to assign definitive conservation ranks and priorities to rare plants, hence the placement of many poorly known taxa on CNPS List 3 (list of plants about which we need more information) in the *Inventory*. Lastly, poorly known or recently discovered taxa are often assumed by opponents of endangered species protection to occur in other areas and therefore to be too common for concerted protection efforts. In certain cases they are correct. Although Federally listed as a threatened species in 1990, recent field surveys have revealed that *Eriastrum hooveri* is considerably more common in the San Joaquin Valley than previously thought, and it is already a candidate for delisting. During the recent listing process that provided California Endangered Species Act protection to *Ceanothus ophiochilus*, opponents repeatedly challenged biologists' knowledge of the plant's distribution, and correctly argued that other populations might exist in addition to the lone known locality at Vail Lake in Riverside County. That two additional small populations were discovered nearby is unsurprising given the very recent description of the species, but both this and *Eriastrum hooveri*'s relative abundance vis-a-vis our lower estimates underscore the need for additional field and herbarium surveys for many of California's rare and endangered plants.

Our ignorance of the relative abundance and distribution of many species both common and rare tends to be hidden in the broad statements about species range that occur in statewide and regional floras. Many rare plants are so poorly known that their rarity remains obscure, and only floristic field work which considers the status and distribution of all species within the study area will reveal these rarities. We need more broadly based floristic field work and collecting!

TABLE 3. COMPILED DISTRIBUTIONAL RESEARCH NEEDS FOR THE RARE FLORA OF CALIFORNIA. Criteria for inclusion are discussed in the text. Consult Hickman (1993), Skinner and Pavlik (1994), and the CNPS Rare Plant Program for more information about each entry.

†M. Authors of *The Jepson Manual* treatment. * Research completed, but not yet published. † Deceased.

Scientific name	Authorities	Research problem
<i>Abronia maritima</i>	Richard Spellenberg TM	Unknown abundance and vigor in northern portion of distribution and Channel Islands.
<i>Agrostis humilis</i>	M. J. Harvey TM /Kurt R. Neisess	Uncertain distribution and abundance; probably more widespread in CA.
<i>Androsace elongata</i> ssp. <i>acuta</i>	Anita F. Cholewa & Douglass M. Henderson TM	Uncertain distribution and abundance; many historical occurrences extirpated.
<i>Arenaria macradenia</i> var. <i>kuschei</i>	Ronald L. Hartman TM /Tim Ross	Unknown distribution and abundance; known from only a single collection from 1929.
<i>Arnica fulgens</i>	Theodore M. Barkley TM /Stephen R. Downey & Keith E. Denford/William Gruzzo	Uncertain distribution and abundance.
<i>Atriplex serenana</i> var. <i>davidsonii</i>	Dean W. Taylor & Dieter H. Wilken TM /David Bramlet/Craig Reiser	Uncertain distribution and abundance.
<i>Atriplex minuscula</i>	Dean W. Taylor & Dieter H. Wilken TM /John Stebbins	Uncertain distribution and abundance.
<i>Atriplex depressa</i>	Dean W. Taylor & Dieter H. Wilken TM	Uncertain distribution and abundance.
<i>Azolla mexicana</i>	Alan R. Smith TM	Uncertain distribution and abundance; difficult to distinguish from <i>A. filiculoides</i> , which is common.
<i>Boschniakia hookeri</i>	Lawrence R. Heckard† TM	Uncertain distribution and abundance in northern CA and beyond.
<i>Calandrinia breweri</i>	Walter A. Kelley TM	Uncertain distribution and abundance; widespread, but most collections are old.
<i>Calochortus weedii</i> var. <i>vestitus</i>	Peggy Fiedler & Bryan D. Ness TM /H. P. McDonald	Uncertain distribution and abundance in Santa Lucia Mtns.
<i>Calyptridium parryi</i> var. <i>hesseae</i>	Dieter H. Wilken & Walter A. Kelley TM	Uncertain distribution and abundance.
<i>Calyptegea sepium</i> spp. <i>binghamiae</i>	Richard K. Brummitt TM	Uncertain distribution and abundance; possibly extinct.
<i>Cardamine pachystigma</i> var. <i>dissectifolia</i>	Reed C. Rollins TM	Uncertain distribution and abundance.

TABLE 3. CONTINUED

Scientific name	Authorities	Research problem
<i>Caulanthus simulans</i>	Roy E. Buck TM */Andrew C. Sanders	Uncertain distribution due to similarity with <i>C. heterophyllus</i> var. <i>pseudosimulans</i> (unpublished).
<i>Carex comosa</i>	Joy Mastrogiuseppe TM /Glenn Clifton Richard A. Lis TM	Uncertain distribution and abundance, since apparently rarely collected.
<i>Carex sheldonii</i>	Joy Mastrogiuseppe TM	Uncertain distribution and abundance.
<i>Cercocarpus betuloides</i> var. <i>blancheae</i>	Daryl L. Koutnik TM /R. Mitchel Beauchamp James C. Hickman TM /James L. Reveal & Clare Hardham/Steve Boyd/David Bramblet	Unknown distribution on other Channel Islands.
<i>Chamaesyce platysperma</i>		Uncertain distribution and abundance.
<i>Chorizanthe parryi</i> var. <i>parryi</i>		Uncertain distribution and abundance; confused with <i>C. procumbens</i> , and many historical occurrences extirpated.
<i>Collomia corymbosa</i>	Elizabeth Chase Neese TM	Uncertain distribution and abundance.
<i>Epilobium howellii</i>	Peter C. Hoch TM	Uncertain distribution and abundance.
<i>Equisetum palustre</i>	Richard L. Hauke TM	Uncertain distribution and abundance.
<i>Ivesia arizonica</i> var. <i>arizonica</i>	Barbara J. Ertter TM	Uncertain distribution and abundance.
<i>Juncus marginatus</i> var. <i>marginatus</i>	Janice Coffey Swab TM /Barbara Ertter	Distribution poorly documented.
<i>Lessingia hololeuca</i>	Meredith A. Lane TM	Uncertain distribution and abundance; probably relatively widespread.
<i>Lomatium nudicaule</i>	Lincoln Constance TM	Plants from Red Mt., Mendocino Co. vouchered at UC may be this taxon.
<i>Limosella subulata</i>	Margriet Wetherwax TM /Niall McCarten & Roxanne Bitman/Brad Olson	Uncertain relationship to plants from East Coast.
<i>Madia yosemitana</i>	David J. Keil TM /Bruce G. Baldwin	Uncertain distribution and abundance; easily overlooked.
<i>Marsilea oligospora</i>	Alan R. Smith & Thomas Lemieux TM /David M. Johnson	Uncertain distribution and abundance.
<i>Monandrella candidans</i>	James D. Jokers TM	Present distribution poorly documented; many historical occurrences.
<i>Navarretia leucocephala</i> ssp. <i>bakeri</i>	Alva G. Day TM /James D. Jokers TM	Uncertain distribution and abundance; may be more widespread.

TABLE 3. CONTINUED

Scientific name	Authorities	Research problem
<i>Piperia michaelii</i>	Dieter H. Wilken & William F. Jennings ^{JM} /James D. Ackerman/R. Morgan Alan R. Smith & Thomas Lemieux ^{JM} /David Wagner	Uncertain distribution and abundance; probably relatively widespread.
<i>Polystichum lonchitis</i>		Uncertain distribution and abundance.
<i>Potamogeton epihydrus</i> ssp. <i>nut-tallii</i>	Robert F. Thorne ^{JM}	Uncertain distribution and abundance.
<i>Potamogeton filiformis</i>	Robert F. Thorne ^{JM}	Uncertain distribution and abundance; probably relatively widely distributed.
<i>Potamogeton foliosus</i> var. <i>fibrillosus</i>	Robert F. Thorne ^{JM}	Uncertain distribution and abundance; to be expected in Great Basin areas of CA.
<i>Potamogeton praelongus</i>	Robert F. Thorne ^{JM}	Uncertain distribution and abundance.
<i>Potamogeton robbinsii</i>	Robert F. Thorne ^{JM}	Uncertain distribution and abundance.
<i>Potamogeton zosteriformis</i>	Robert F. Thorne ^{JM}	Uncertain distribution and abundance, especially in the Central Valley.
<i>Puccinellia pumila</i>	Jerrold I. Davis ^{JM} /Arthur M. Phillips, III & Barbara G. Phillips	Possibly poorly known or undercollected in CA.
<i>Selaginella densa</i> var. <i>scopulorum</i>	Dieter H. Wilken ^{JM} /Ivan Valdespino/Alan R. Smith	Uncertain distribution and abundance.
<i>Senecio hydrophiloides</i>	Theodore M. Barkley ^{JM}	Uncertain distribution and abundance.

EXTINCT PLANTS, SOME WITH HIGH REDISCOVERY POTENTIAL

As natural habitat in California continues to shrink, it becomes imperative to rediscover populations of plants currently thought to be extinct (Table 4), and to safeguard populations that are found. Comprehensive, properly timed field survey of all remaining habitat for many of California's extinct plants is desirable now, before likely habitat is further degraded or eliminated by development, agriculture, exotic plants or animals, vehicles, or other destructive anthropogenic activities. Searching for extinct taxa can be fruitful: in the period between 1988 and 1994, thirteen taxa were relocated in California.

While some of the plants considered extinct in California are probably permanently gone (e.g., *Howellia aquatilis*, *Potentilla multijuga*; the latter discussed in Ertter 1993), others have high potential for rediscovery (e.g., *Monardella leucocephala*, *Tropidocarpum caparideum*, various *Mimulus* and *Plagiogothrys* spp.), but focused surveys of potential habitat have either not been conducted or have been sporadic or haphazard. Searches must be strategic and exhaustive, should build upon past unsuccessful efforts (consult CNPS for detailed information about protocols and search history), and should be conducted when plants are most visible and identifiable. Investigations should emphasize known localities with remaining habitat and nearby areas with appropriate vegetation and soils. Timing is critical since a high percentage of the plants in Table 4 are annuals (Pavlik and Skinner 1994) which may appear only in favorable wet years; searches in inauspicious years may be pointless. For example, a single plant of *Trifolium amoenum* was recently rediscovered in Sonoma County in May 1993 (Conners 1994), following the wettest winter in California in a decade.

Careful consideration of Table 4 reveals two noteworthy trends. Five of the 32 California plants that are presumed extinct occurred on the Channel Islands. This disproportionate representation is almost certainly linked to more than a century of devastating overgrazing practices and debilitating competition from exotic grassland plants. It remains distinctly possible that some of these taxa persist as seeds in the soil, and as overgrazing is controlled or eliminated on the Channel Islands some of these taxa may reappear. Twelve of the presumptive extinctions are known only from their type locality in California or its immediate vicinity, including nine known from only the type collection. Many of these taxa must be considered taxonomically suspect (e.g., *Castilleja uliginosa* and *Mimulus bran-degei*). This is because adequate taxonomic comparisons are difficult or impossible with scant material for study, raising the likelihood that some of these taxa were described from aberrant or unusual

TABLE 4. EXTINCT PLANTS IN CALIFORNIA, SOME WITH HIGH REDISCOVERY POTENTIAL. Consult Hickman (1993), Skinner and Pavlik (1994), and the CNPS Rare Plant Program for more information about each entry, including details of recent rediscovery attempts. ¹ Known only from the type locality and immediate vicinity. ² Known only from the type collection. ³ Extant outside California.

Scientific name	Last seen	Notes
<i>Arcostaphylos hookeri</i> ssp. <i>franciscana</i>	1942	Known from only three occurrences in San Francisco; now occurs only in cultivation. Exirpated by residential development.
<i>Astragalus mojavensis</i> var. <i>hemigrusso</i>	1941	Known in CA from only one collection from Darwin Mesa, Inyo Co. First collection in NV since 1939 made near type locality in 1985.
<i>Astragalus pycnostachys</i> var. <i>lanosissimus</i>	1967	Habitat lost to urbanization. Recent attempts (including 1987) to rediscover this plant have been unsuccessful.
<i>Calochortus monanthus</i> ²	1876	Known only from the type locality along the Shasta River, Siskiyou Co. Now mostly converted to agriculture; site degraded by overgrazing and non-native plants. Field surveys in 1990 and earlier unsuccessful.
<i>Carex livida</i>	1866	Known in CA from only one collection near Mendocino City, Mendocino Co. Field surveys unsuccessful. Local experts doubt potential for rediscovery.
<i>Catilleja uliginosa</i>	1987	Known from two occurrences in Pitkin Marsh and Trembley's Marsh, Sonoma Co. Last known remaining plant died in 1987, despite management efforts. No access allowed by landowner after 1987.
<i>Chorizanthe parryi</i> var. <i>fernandina</i>	1940	Most historical habitat is now heavily urbanized. Numerous recent field surveys have been unsuccessful; most likely to be rediscovered in northwestern Los Angeles Co., especially in the Elizabeth Lake area.
<i>Dissanthelium californicum</i>	1912	Known in CA from only two occurrences on San Clemente and Santa Catalina Islands. Possibly extirpated by feral goats.
<i>Erigeron mariposanus</i>	1900	Collected several times from 1892–1900; localities vague. Suspected to occur in specialized habitats.
<i>Eriogonum truncatum</i>	1940	Much habitat eliminated by grazing and urbanization. Recent field surveys (including 1985–1987) unsuccessful.
<i>Eschscholtzia rhombipetala</i>	1950	Field surveys in 1986, 1980, and earlier unsuccessful. Report from La Panza, San Luis Obispo Co. probably misidentified <i>E. lemmonii</i> ssp. <i>lemmonii</i> .
<i>Helianthus nuttallii</i> ssp. <i>parishi</i>	1937	Exirpated by destruction of marsh habitat by urbanization. Most likely to be rediscovered near Seven Oaks, San Bernardino Co.

TABLE 4. CONTINUED

Scientific name	Last seen	Notes
<i>Howellia aquatilis</i> ○	1928	Known in CA from only one collection near Howard Lake, Mendocino Co. Possibly extirpated by cattle grazing and trampling. Numerous rediscovery attempts (1975, 1979, 1980, and more recent) unsuccessful.
<i>Lycium verrucosum</i> †	1901	Known only from the type collection on San Nicolas Island; locality vague. Field surveys (including 1978 and 1979) unsuccessful.
<i>Malacothamnus mendocinensis</i>	1939	Known from only two collections near Ukiah, Mendocino Co. Recent intensive field surveys unsuccessful.
<i>Malacothamnus parishii</i> †	1895	Only known from the type collection in San Bernardino Valley, San Bernardino Co. Extirpated by urbanization. Field surveys unsuccessful.
<i>Mimulus brandegei</i> ‡	1932	Known from only two collections on Santa Cruz Island. Possibly extirpated by grazing. Field surveys prior to 1979, in 1985, and 1992 unsuccessful.
<i>Mimulus traskiae</i> §	1904	Known only from the type collection near Avalon; locality vague. Possibly extirpated by grazing or development.
<i>Mimulus whipplei</i> †	1854	Known only from the type collection near Murphys, Calaveras Co. Many recent field surveys unsuccessful.
<i>Monardella leucocephala</i>	1941	Known from only three occurrences. Probably extirpated by agricultural conversion. Field surveys in 1986 unsuccessful, but high potential for rediscovery.
<i>Monardella pringlei</i> †	1921	Known from only two occurrences in the vicinity of Colton. Habitat lost to urbanization. Many recent field surveys unsuccessful.
<i>Montia howellii</i> ○	1933	Known in CA from seven collections. Field surveys in 1989 and 1992 in CA unsuccessful; recent surveys located new populations in OR and WA. Sometimes mistaken for <i>M. fontana</i> or <i>M. dichotoma</i> .
<i>Ophioglossum pusillum</i> ○	1894	Known in CA from only two occurrences.
<i>Orthocarpus pachystachys</i>	1913	Known from only two collections, localities vague. Probably extirpated by agriculture and grazing.
<i>Phacelia cinerea</i> †	1901	Known only from the type collection on San Nicolas Island. Field surveys in 1977–1979 and others since 1983 unsuccessful.
<i>Plagiobothrys glaber</i>	1954	All collections since 1930's located in the Hollister area; plant should be looked for there. Possibly a variety or ecotype of <i>P. stipitatus</i> .

TABLE 4. CONTINUED

Scientific name	Last seen	Notes
<i>Plagiobothrys hystericulus</i> ^T	1892	Known only from the type collection in the Montezuma Hills; all other reports misidentifications. Easily confused with <i>P. acanthocarpus</i> , <i>P. trachycarpus</i> , and others.
<i>Plagiobothrys lithocaryus</i> ^T	1899	Known only from the type collection from Lakeport, Lake Co. in 1884 and an uncertain collection from Potter Valley, Mendocino Co. in 1899; should be looked for in these areas.
<i>Plagiobothrys mollis</i> var. <i>vestitus</i> ^T	1888	Known only from the type collection near Petaluma. Thought to be extirpated by agriculture in 1932.
<i>Poliominta incana</i> O	1938	Known in CA from only one occurrence at Cushenbury Springs. Possibly extirpated by mining activities.
<i>Potentilla multijuga</i> L	1890	Known only from one occurrence near Ballona, Los Angeles Co. Extirpated by urbanization. Recent field surveys unsuccessful.
<i>Tropidocarpum caparideum</i>	1957	Field surveys (1974, 1978, 1979, 1981, 1986, 1987) unsuccessful.

representatives of more widespread close relatives. Barring discovery of new populations, confirmation of taxonomic independence for these taxa is unlikely.

CONCLUSION

Only time will tell whether it is possible for anyone to monitor the progress of rare plant research in California as we are attempting to do here. It is an enormous state with many contributing lay and professional researchers and conservationists, and with more than its share of complex botanical problems. Whether we are successful in addressing current problems and maintaining an active understanding of research needs for plant conservation in California depends solely on the participation of all who study our declining flora. We hope readers will send any information they currently possess which has bearing on the many and sometimes controversial problems outlined here to the CNPS Rare Plant Program; all such information is used jointly by the NDDB. We hope botanists will publish results of completed or long dormant studies. We also hope that researchers will seize upon the problems presented here for both their inherent scientific interest and immediate conservation applications.

So, focus your research on problems of conservation importance. Submit grant requests to CNPS and other organizations. Do the research, now. The fourth edition of the *Inventory* (Smith and Berg 1988) included 675 taxa on List 1B, the plants which are rare and endangered in California and everywhere else. The fifth edition includes 857 List 1B plants, a 27% increase in only six years. We are truly running out of time to establish and implement plant conservation priorities in California.

ACKNOWLEDGMENTS

We appreciate the learned suggestions of Steven W. Edwards, James D. Jokerst, Jon E. Keeley, Dale W. McNeal, Timothy C. Messick, Robert Ornduff, and Dieter H. Wilken.

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(Received 13 Sep 1994; accepted 10 Feb 1995)

OVERVIEW OF THE BUREAU OF LAND MANAGEMENT

JOHN WILLOUGHBY

Bureau of Land Management, California State Office,
2800 Cottage Way, Sacramento, CA 95825

MISSION AND ROLE OF THE BUREAU OF LAND MANAGEMENT

The Federal Land Policy and Management Act of 1976 (FLPMA) is the principal law guiding the management of Bureau of Land Management (BLM) lands. The BLM is committed to safeguarding the ecological sustainability of the public lands under its care. By implementing management that conserves the diversity and protects the integrity of the land, the BLM will ensure that present and future generations continue to derive economic, recreational, social, cultural, and aesthetic benefits from public lands.

GENERAL ORGANIZATIONAL STRUCTURE

BLM-California is organized along a “grass roots” structure, with 20 offices throughout the State near the public lands they administer. The backbone of this organizational structure are the 15 area offices, each led by an area manager and a staff of resource specialists. These resource areas are organized into 4 districts, which provide them administrative support and regional guidance. At the top level is the BLM California State Office, headed by State Director Ed Hastey.

The BLM in California employs 10 persons classified formally as botanists. In addition to these botanists, there are 4 personnel classified in other series (e.g., range conservationists, natural resource specialists) who work in floristics and rare plant conservation.

BLM-California is in the process of restructuring the staffs at the three levels of the organization. The goal is to put more people at the resource area level by reducing or eliminating duplicative functions at higher levels. Office locations are expected to stay the same.

SCOPE OF BUREAU OF LAND MANAGEMENT RESPONSIBILITIES FOR PLANT CONSERVATION

The BLM manages nearly 17.2 million acres of public lands in California in almost every one of California’s 58 counties. The plant communities managed by California-BLM are extremely diverse. A majority of the natural communities described in Holland’s *Preliminary Descriptions of the Terrestrial Plant Communities of California* are represented on BLM lands in the State. On the public lands of the California Desert Conservation Area (a 25 million acre area in

the Mojave and Colorado deserts of California, which includes 12.5 million acres of BLM lands), 2179 species, subspecies, and varieties of vascular plants have been catalogued.

BLM lands in California support the following numbers of special status plant species: Federal Endangered—12; Federal Threatened—4; Federal Proposed—12; Federal Candidate and CNPS List 1&2 Plants—168; totaling 196 species. In addition to the species that are known to occur on BLM lands, we suspect that another 137 species may occur on BLM lands. Further inventory is required to confirm or reject this.

Of those special status plants that occur on BLM lands, about 30 species are restricted or nearly restricted to BLM lands, and another 40 species have half or more of their total distribution on BLM lands. Some of the more important BLM occurrences, however, are of species that occupy mostly private lands; because of development of the private lands, the BLM lands offer some of the only remaining refuges for these species.

HIGHLIGHTS OF CURRENT CONSERVATION ACTIVITIES

Inventory. Inventory remains a critical need for the BLM in California. Considerable effort is being directed to the San Joaquin Valley because of the many listed and candidate plant species in the area and the need for information to guide ecosystem management in the Valley. Three species-directed inventories have been completed by Russ Lewis of the Caliente Resource Area in Bakersfield. These, in combination with work done by other Bakersfield District botanical staff, have documented 377 new occurrences of *Antirrhinum ovatum*, 627 new occurrences of *Eriastrum hooveri*, and 535 new occurrences of *Lembertia congdonii*. Also in the San Joaquin Valley, the number of known occurrences of *Caulanthus californicus* has been increased by 17.

The Bishop Resource Area has been conducting rare plant surveys in several areas, including the Bodie Hills Management Area (2200 acres), the Inyo Mountains Area of Critical Environmental Concern (1000 acres), and Slinkard Valley (300 acres). In addition to discovering new occurrences of several special status plants, preliminary plant lists have been compiled and voucher collections made.

Our California Desert District has documented new occurrences of many rare plant species, including *Penstemon calcareous* (10 new occurrences) and *Maurandya antirrhiniflora* ssp. *antirrhiniflora* (8 new occurrences), found as a result of a cooperative survey involving the California Native Plant Society.

Both the Ukiah and Susanville districts have been involved in inventory efforts that have resulted in the discovery of several new occurrences of special status plants.

Monitoring. Most monitoring by BLM personnel in California consists of returning to known sites, observing any threats, filling out California Natural Diversity Data Base Field Survey Forms, and possibly estimating the number of individuals using a logarithmic scale (1–10, 10–100, 100–1000, etc.). Several quantitative monitoring studies are conducted regularly, including the following.

Long-term monitoring of rare plant taxa, including the endangered *Arabis mcdonaldiana*, on Red Mountain, Mendocino County, has been conducted by Dr. Michael Baad through a cooperative agreement with BLM.

Monitoring of *Camissonia benitensis* in San Benito County has taken place for many years, both by BLM personnel and by contract with BioSystems Analysis.

Two rare plants, *Chlorogalum grandiflorum* and *Lomatium nudicaule*, found in the Red Hills, Tuolumne County, have been monitored, both inside and outside grazed areas, since 1984.

Restoration. Several efforts are being made to restore native plant habitat. BLM is cooperating with The Nature Conservancy to eradicate alien plants in the Samoa and Manila dunes of Humboldt County and restore habitat of *Erysimum menziesii* and *Layia carnosa*. A total of \$45,000 will be committed this fiscal year to this effort.

Considerable work is being done to remove introduced species of the genus *Tamarix* from riparian areas and oases in the Mojave and Colorado deserts. This year's efforts are concentrated on Afton Canyon and Dos Palmas.

The Susanville District is developing a native plant restoration program, promoting reclamation with local native species. The District is in the process of establishing its own native grass seed source (using locally collected seeds) in association with the necessary reclamation of a proposed buried pipeline.

Studies. BLM is supporting demographic studies being conducted by the U.S. Fish and Wildlife Service of three listed San Joaquin Valley plant species. Grazing impacts on these species are also being investigated.

Education. BLM conducts numerous field trips and natural history talks, both in the field and in schools and communities. Interpretive signs and kiosks also help spread the word about the importance of conserving the rich floristic heritage of California's public lands.

ADEQUACY OF KNOWLEDGE OF SPECIAL STATUS PLANTS

Despite considerable effort in inventorying and monitoring its special status plants, California-BLM is a long way from realizing its goal of complete knowledge of the distribution and status of the

special status plants on BLM lands. The scattered nature of the public lands to the west of the Sierra Nevada and north of the Tehachapi Mountains makes inventory extremely difficult.

In 1991 BLM-California estimated that only 11 percent of its public lands had been adequately inventoried for special status plants, that only 6 percent of its special status plants were being monitored, and that only 4 of 65 needed studies had been completed. The situation is only slightly better today.

Greater effort will be required to more thoroughly understand the rare flora of the public lands in California. The BLM, together with all those interested in the conservation of special status plants, must try even harder to gather the information required to develop ecosystem management plans that truly conserve the State's rare plants and natural plant communities.

(Received 7 Oct 1994; accepted 20 Jan 1995)

OVERVIEW OF THE U.S. FISH AND WILDLIFE SERVICE

JAN C. KNIGHT

U.S. Fish and Wildlife Service, Sacramento Field Office,
2800 Cottage Way, Room E-1803, Sacramento, California 95825

MISSION AND ROLE OF THE FISH AND WILDLIFE SERVICE

The mission of the Fish and Wildlife Service is to conserve, protect, and enhance fish and wildlife and their habitats for the continuing benefit of the American people. The Fish and Wildlife Service has regulatory authority and enforcement responsibility: Endangered Species Act administration; migratory birds (Migratory Bird Treaty Act); certain marine mammals (Marine Mammal Protection Act); National Wildlife Refuges (National Wildlife Refuge Systems Administration Act of 1966); interstate and international fishery resources; fish and wildlife grant program administration (Wetlands Reserve Program, Section 6 Endangered Species Act); mapping wetlands of the U.S. and providing wetland information for planning purposes (National Wetlands Inventory); enforcement of Endangered Species Act and Migratory Bird Treaty Act; inspection of imports to protect fish, wildlife, and plants.

The Fish and Wildlife Service has review authority or provides technical assistance and expertise on fish and wildlife and their habitats in the following areas: 1) On water resources development projects for Bureau of Reclamation, U.S. Army Corps of Engineers, or Soil Conservation Service (Fish and Wildlife Coordination Act); 2) on permit proposals for wetlands permits issued by the U.S. Army Corps of Engineers, and for hydropower licensing by the Federal Energy Regulatory Commission (Fish and Wildlife Coordination Act in concert with Clean Water Act, Rivers and Harbors Act, Federal Power Act); 3) to other Federal, state, and public agencies on effects of environmental contaminants, and in remediation of adverse contaminant effects, on fish and wildlife resources (Migratory Bird Treaty Act, Clean Water Act, Federal Environmental Pesticide Control Act, Superfund, Oil Pollution Act); 4) support and coordination in coastal areas in implementing management, restoration, and protection of coastal ecosystems (Bay/Estuary Program); and 5) technical assistance for conservation and restoration of wetlands and associated upland habitats in support of Farm Bill (Food Security Act).

GENERAL ORGANIZATIONAL STRUCTURE

The Fish and Wildlife Service is a Federal agency in the Department of the Interior. The Director and Deputy Director are political appointees having background or experience in resource management. Decision-making is delegated primarily to the Regional and field office levels.

The Service is administratively organized into 7 geographic regions. California is in Region 1, which also includes Hawaii, Oregon, Washington, Nevada, and Idaho. Region 1 headquarters are in Portland, Oregon.

The Service employs 11 full-time botanists in California. Ten are in the Division of Endangered Species and 1 is in the Division of Water Resources.

The Service manages approximately 91 million acres in the National Wildlife Refuge System, making it the third largest Federal landholder after Bureau of Land Management and Forest Service. Land ownership by the Service is restricted to lands in the National Wildlife Refuge System, or fish hatchery facilities.

The majority of agency functions described above are not derived from its land management responsibilities and typically are administered out of field offices distributed throughout the regions, generally 1 per state. California's three field offices are located in Sacramento, Ventura, and Carlsbad.

Sacramento Field Office is responsible for the Central Valley to the crest of the Tehachapis and coastal counties from Santa Clara

north; Ventura is responsible for the east side of the Sierras, northern Mojave, and coastal counties from Santa Cruz to Ventura; Carlsbad is responsible for southern California from approximately Los Angeles and Riverside Counties south.

SCOPE OF FISH AND WILDLIFE SERVICE RESPONSIBILITIES FOR PLANT CONSERVATION

The Service's most significant role in plant conservation lies in its responsibility for Endangered Species Act implementation and administration. Agency conservation functions under this law include candidate species assessment, listing/delisting/reclassification, recovery planning, technical assistance, cooperation with the states, Federal agency consultations, habitat conservation planning, and permits.

California currently has 47 listed endangered and 5 listed threatened plant species; 42 proposed endangered and 16 proposed threatened plant species; and 621 candidate plant species. California is second only to Hawaii in total number of listed plants.

Approximately 60 federally listed plants have been identified on National Wildlife Refuge System lands nationally. In California, the San Francisco Bay National Wildlife Refuge manages nearly all remaining habitat for 2 listed plants, Antioch Dunes evening-primrose and Contra Costa wallflower. At least 6 other listed or proposed plants are known from refuge lands in California. Complete botanical inventories do not exist for California's refuges, however, and the extent of rare plant populations they actually support is unknown. Recent agency emphasis on ecosystem management may direct funding to inventories and encourage heightened management awareness of rare plant resources on refuge lands.

HIGHLIGHTS OF CURRENT CONSERVATION ACTIVITIES

The Service contributed nearly \$339,000 to the California Department of Fish and Game in 1994 for cooperative plant conservation projects under Section 6 of the Endangered Species Act. This is an all-time high for Fish and Game's Endangered Plant Program. California's rare plants should continue to benefit from new guidelines for allocating Section 6 funds that consider the total number of listed and candidate species as well as conservation benefit of a project, rather than financial parity between states.

(Received 7 Oct 1994; accepted 20 Jan 1995)

OVERVIEW OF THE NATIONAL PARK SERVICE

SARAH G. ALLEN

National Park Service, Western Region,
600 Harrison Street, Suite 600, San Francisco, CA 94107

MISSION AND ROLE OF THE NATIONAL PARK SERVICE

The enabling legislation of the National Park Service in 1916 stated that:

"The Service thus established shall promote and regulate the use of Federal areas known as national parks, monuments, and reservations . . . by such means and measures as conform to the fundamental purpose . . . to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations (NPS Organic Act, 16 USC 1)."

"The National Park Service will manage the natural resources of the national park system to maintain, rehabilitate and perpetuate their inherent integrity."

The vegetation management policy is designed to perpetuate native plant life as part of natural ecosystems. The concept of managing in the context of entire ecosystems is critical to the long-term preservation of national park lands. Ecosystem management is a guiding principle of national park management.

GENERAL ORGANIZATIONAL STRUCTURE

The National Park Service (NPS) is a decentralized organization within the Department of Interior organized at three levels of authority: the Washington office, 10 regional offices, and the individual park units. The basic unit is the park staff, and the assignment of responsibilities among employees reflects the essential functions: cultural and natural resource management, protection of park resources and park visitors, visitor services and interpretation, maintenance of facilities and administration support services. The regional office is the instrument through which the Director can communicate with 343 field areas, and vice versa, managing over 76 million acres. The Washington Office, administered by a Director, develops general policies and standards, sets priorities, and coordinates servicewide resource management and research programs. Prior to their transfer to the National Biological Service, the Western Regional office operated 5 cooperative research study units, asso-

ciated with universities. These include 20 scientists, 4 of which are full-time botanists in California.

The number of full-time employees in the National Park Service in California is around 700. Of these, around 10 are full-time botanists, or whose duties are primarily as botanists, augmented by several seasonal botanists. The number is woefully inadequate.

The Western Region administers 43 national parks, monuments, historic sites, national seashores, national rivers and trails and national recreation areas in four states and two territories. The office is responsible for the states of Arizona, California, Hawaii and Nevada, and the territories of Samoa and Guam. The lands comprise 8 million acres with a diversity of habitats. Western Region has more listed species than all the other regions. The National Park Service manages 4.7 million acres in California, which provide habitat for more than 300 special status plants.

Within a park, management of natural systems is based on zones; natural zones (natural resources managed with a concern for fundamental ecological processes as well as for individual species), cultural zones (preserve cultural resources), and park development zones (intensive visitor use).

In addition, NPS is responsible for lands with special designation. National parks in the WR administer Wilderness Areas in 22 national park units, including nearly 3 million acres. Also there are 67 National Natural Landmarks (NNL) in the Western Region, 34 of which occur in California. These lands, although often held privately, are given special recognition by NPS because of natural features that are deemed nationally significant. Examples of NNL lands in California include Nipoma Dunes and Consumnes River Preserve. Individual park ecosystems that are components of regional ecosystems believed to be internationally significant may be designated as Biosphere Reserves administered by the Man and the Biosphere Program under UNESCO; there are six in California. Examples include the Mojave Desert, central coastal California, and Sequoia/Kings Canyon NP. World Heritage sites are also designated under UNESCO and administered by NPS; there are two in California (Redwood NP and Yosemite NP).

SCOPE OF NATIONAL PARK SERVICE RESPONSIBILITIES FOR PLANT CONSERVATION

Legal mandates for plant conservation in NPS include the National Environmental Policy Act, Wilderness Act, Endangered Species Act of 1973, and Organic Act of 1916.

The objective of NPS for plant conservation is to perpetuate native plant life as part of natural ecosystems. Landscapes and plants may be manipulated to restore or enhance the functioning of the plant

and animal community, or to benefit threatened, endangered and sensitive species.

Revegetation Program. The Western Region has a directive to promote revegetation throughout all parks. Revegetation efforts in natural zones will use natural regeneration, and seeds or transplants representing species and gene pools native to the ecological portion of the park where the restoration project occurs.

Fire monitoring program. Prescribed and natural fires contribute to the conservation of plants by restoring an area to a natural range of conditions. Reseeding efforts after fires are discouraged, as in the case of the 1993 fire in Santa Monica Mountains NP.

Threatened, endangered and sensitive species (TES) program. This program identifies and promotes the conservation of all federally listed TES species and state and locally listed threatened, endangered, rare, declining, sensitive or candidate species that are native to and present in the parks, and their critical habitats. All special status species are given the same protection as federally listed species. Administratively, this program has a TES coordinator at each level of NPS from Washington to individual park units.

Inventory and monitoring program. The policy of NPS is to assemble baseline inventory data describing the natural resources under its stewardship, to monitor these resources forever, to detect or predict changes that may require intervention, and to provide reference points for comparisons. A guide to this program is presented in NPS-75 (1992).

Alien species management program. This program places high priority on the management of alien species that have a substantial impact on park resources and that can reasonably be expected to be controlled.

HIGHLIGHTS OF CURRENT CONSERVATION ACTIVITIES

Inventory and monitoring program. This involves 1) a Servicewide vegetation mapping of all NPS lands and creation of a nationwide classification system, and 2) the development of a database of native plants occurring on NPS land (NPFLORA). The database will include information on systematics, distribution and abundance, and curation. Ultimately, this program will link into a geographic information system.

Restoration projects. Major restoration projects are occurring in many parks in California. Examples include watershed restoration for over 15 years at Redwood NP using innovative technologies; proposed restoration of the Giant Forest in Sequoia/Kings Canyon

NP by removing 50 years of infrastructure and restricting cars; and Lake Merced restoration at Yosemite NP.

Native plant propagation. This is occurring at 12 parks in California. For example, Aberdeen Plant Materials Center entered into an agreement with Lava Beds NM to produce seed and plants of native plant species for revegetation purposes and to develop propagation methods. Joshua Tree National Monument has an arid lands restoration center.

Celebrating wildflowers. This is a collaborative commemoration between several federal land management agencies to promote the importance of conservation and management of native plants and plant habitats.

Volunteer activities in parks have contributed substantially in plant conservation and education. For example, at Golden Gate NRA alone, over 10,000 volunteer hours have been devoted to plant restoration projects at more than 40 sites. Golden Gate NRA has also initiated a Site Stewardship program to foster long-term efforts for groups of volunteers at specific sites.

The Western Region is involved in several interagency committees and task groups in California such as the Executive Council on Biodiversity, bioregional councils, and the Sierra Nevada Ecosystem Project.

(Received 7 Oct 1994; accepted 20 Jan 1995)

OVERVIEW OF THE USDA-FOREST SERVICE

JAMES R. SHEVOCK

USDA-Forest Service, Pacific Southwest Region,
630 Sansome Street, Room 823, San Francisco, CA 94111

THE MISSION AND ROLE OF THE FOREST SERVICE

By law, the Forest Service is required to manage national forest resources for water supply, recreation opportunities, wildlife habitat, timber, range, and other renewable uses. Many goods and services provided are sold or are subject to user fees.

The phrase "CARING FOR THE LAND AND SERVING PEOPLE", captures the Forest Service mission. As set forth in federal

law, the mission is to achieve quality land management under the sustainable multiple-use concept to meet diverse needs of people. It includes: Advocating a conservation ethic in promoting the health, productivity, diversity and beauty of forests and associated lands; developing and providing scientific and technical knowledge aimed at improving our capability to protect, manage, and use forests and rangelands; and protecting and managing the National Forests and Grasslands so they best demonstrate the sustainable multiple-use management concept.

GENERAL ORGANIZATIONAL STRUCTURE

The Forest Service, established in 1905, is a decentralized agency within the U.S. Department of Agriculture where decisionmaking is delegated to the lowest level appropriate in the organization. The Forest Service is administered by a Chief and Associate Chief in Washington, DC. The top leadership is made up of career civil servants versus political appointees.

Programs are developed into six areas administered by a Deputy Chief. These areas are the National Forest System, International Forestry, Research, State and Private Forestry, Programs and Legislation, and Administration. Under each Deputy Chief are Staff Directors who administer specific functional program areas such as Wildlife, Fish and Rare Plants, Minerals and Geology, Range Management, Timber Management, Recreation, Heritage, and Wilderness Management and so forth.

The Forest Service is comprised of 9 Regions, each administered by a Regional Forester, 8 Research Stations administered by a Director, and an Institute of Tropical Forestry (in Puerto Rico).

The Forest Service administers 156 national forests and 20 grasslands in 44 states. These lands comprise 191 million acres with an amazing variety of habitats, from subarctic tundra to tropical rain forest amounting to nearly 8 percent of the land in the United States. Over 10,000 plant species are suspected to occur on the national forests and grasslands.

The Pacific Southwest Region of the Forest Service manages 18 national forests and one grassland in California (with small acreages extending into southern Oregon and western Nevada), comprised of 20 million acres which is 20 percent of the state land base. It is predicted that the national forests and grassland provide habitat for over two-thirds of the California flora. Complete floras and/or checklists for national forests are not available. Many new species are still being discovered on the national forests in California. The Pacific Southwest Region also covers Hawaii, Guam, and Trust Territories of the Pacific Islands where technical assistance is pro-

vided by a Pacific Islands Forester as part of the Region's State and Private Forestry program area.

Special designated lands are important units of managing the national forests. National forests in California administer 54 Wilderness areas (under the Wilderness Act of 1964, as amended) covering 4.4 million acres, nearly 20 percent of the national forest land base in California. Under the provisions of the Wild and Scenic Rivers Act of 1968, over 958 miles of rivers have been designated as wild, scenic, or recreational on the National Forests in California.

Special Interest Areas (which include botanical areas) is a land allocation used to conserve areas with high species diversity, unique assemblages, habitat types etc. Nearly 100 Special Interest Areas have been established to protect, and where applicable, foster public enjoyment of areas with scenic, historical, geological, botanical, zoological, or other special attributes. Examples of botanical areas are the Ancient Bristlecone Pine Forest and Butterfly Valley *Darlingtonia* Area.

The remaining land allocation which conserve species and habitats is Research Natural Areas (RNA). These lands preserve a wide spectrum of representative pristine areas that typify important forest, shrubland, grassland, aquatic, alpine, geological and other areas for scientific study. Over 36 RNA's are established in the Pacific Southwest Region.

SCOPE OF FOREST SERVICE RESPONSIBILITIES FOR PLANT CONSERVATION

Two federal laws are primary in plant conservation in the Forest Service. The first is the National Forest Management Act of 1976 (and subsequent regulations) which provide for viable populations and biological diversity. The second is the Endangered Species Act of 1973 (as amended). In addition, policy is contained in the Forest ESA Service Manual (FSM) 2670 chapter which provides for the management of threatened, endangered, and sensitive species (TES).

Every Species Counts! is the program dedicated to conserving TES species on the national forests. TES species are the rarest of our renewable natural resources. Management and conservation of these species is one of the Forest Service's primary land stewardship responsibilities.

The Sensitive Plant Program is the botanical component of Every Species Counts! This program manages over 300 sensitive native California plants, many of them known to occur in fewer than 15 locations. Nearly 100 of these plants are restricted to the national forests in California, and dozens more have the majority of their distribution on the national forests. Conservation strategies are being developed to provide for species viability through time.

Over 90 percent of these sensitive species are identified as list 1B in the 5th edition of the California Native Plant Society's *Inventory of Rare and Endangered Vascular Plants in California* (Skinner and Pavlik 1994). In addition, most of the sensitive plants in the Region are identified as candidate 1 or 2 taxa by the USFWS.

The Pacific Southwest Region of the Forest Service in California has 12 plants listed under the ESA, and 14 species are proposed. Twenty-three state endangered and two state threatened species are listed under the State of California ESA of 1984, and 28 species are listed as rare under the authority of the California Native Plant Protection Act.

HIGHLIGHTS OF CURRENT CONSERVATION ACTIVITIES

The Pacific Southwest Forest and Range Experiment Research Station is increasing its interest and commitment in conservation of TES species. The station has created the Institute of Forest Genetics and the Center for Genetic Conservation.

The National Forest Genetic Electrophoresis Lab has undertaken several sensitive plant projects to determine distinctions between species, and supply evidence for taxonomic recognition of species.

Celebrating wildflowers. This is a collaborative commemoration between several federal land management agencies to promote the importance of conservation and management of native plants and plant habitats and emphasizes the aesthetic, recreational, biological, medicinal, and economic values of wildflowers.

During Fiscal Year 1993, volunteers added significantly to the development of the sensitive plant program. Over 2261 hours of service were donated to the program.

Botanical staffing for the Pacific Southwest Region includes 25 full-time botanists. This workforce is augmented with over 60 botanists during the field season. Due to the nature of administering national forests and grasslands, the Forest Service work force is highly diverse in skills, educational careers and work responsibilities ranging from natural sciences to social sciences. The work force is comprised of over 5000 employees in California.

The knowledge base regarding the presence and status of 300 TES plants ranges from well known to provisional. The strategy employed is to utilize all existing information to determine priority field work and surveys to accomplish each year. For example, during FY 92 the Region documented 414 new occurrences representing 77 sensitive plant taxa. The trend was similar in FY 93 with 340 new occurrences representing 79 plant taxa. In addition, several newly described rare plants have been located on the national forests which focuses our efforts to document their distribution and determine if special management is required to conserve these species.

Once the distribution is fairly well determined, the forest botanist (working with other resource professionals) develops interim prescriptions to reduce impacts to plant occurrences. As ecological information becomes available through conservation assessments, species and/or habitat management guides are prepared. These guides function as conservation strategies and are the basis for maintaining viable populations through time.

The goal of the Forest Service is to become a multicultural and diverse organization representing the American people we serve and responding to their diverse needs through the conservation of natural resources for today and for future generations.

(Received 7 Oct 1994; accepted 20 Jan 1995)

OVERVIEW OF THE CALIFORNIA DEPARTMENT OF FISH AND GAME

SANDRA C. MOREY

California Department of Fish and Game, Natural Heritage
Division 1416 Ninth Street, Sacramento, CA 95814

MISSION AND ROLE OF THE CALIFORNIA DEPARTMENT OF FISH AND GAME

The mission of the Department of Fish and Game is to manage California's diverse fish, wildlife, and plant resources, and the habitats upon which they depend, for their ecological values and for their use and enjoyment by the public. As California's primary trustee agency for fish, wildlife, and plants, the Department actively seeks protection of these resources and their habitats. Because the Department does not have land use authority, it must work cooperatively with federal, state, and local governments, businesses, conservation organizations, and citizens to carry out its mission.

GENERAL ORGANIZATIONAL STRUCTURE

The Department is part of the California Resources Agency. Headquarters is located in Sacramento and consists of the Directorate, divisions, and branches. Divisions and branches carry out specific program functions. Five regional offices carry out program responsibilities in specific geographic areas of the state.

The Director is appointed by the Governor, and is responsible to the Fish and Game Commission for conduct of the Department in accordance with Commission policies. The Fish and Game Commission is a governor appointed body responsible for adopting policies and regulations by which the Department operates. The Department has 1800 full-time employees. Sixteen of these are botanists.

SCOPE OF FISH AND GAME RESPONSIBILITIES FOR PLANT CONSERVATION

The legal framework and authority for the Department's work to conserve plants comes from the California Endangered Species Act (CESA), the Native Plant Protection Act (NPPA), the California Environmental Quality Act (CEQA), and the Natural Communities Conservation Planning Act (NCCPA). The Department works to conserve plants under these laws through listing, habitat acquisition and protection, review of local land use planning, multispecies conservation and recovery planning, research, and education.

The Department's four full-time staff of the Endangered Plant Program work to protect, manage, and recover the State's 215 rare, threatened, and endangered plants.

Four botanists within the Natural Diversity Data Base (NDDB) track location and status information on 1751 rare plant taxa and 135 rare natural communities. This information comes from field survey forms sent to the Data Base by consultants, agency personnel, academics, and amateur botanists.

The Department administers 784,000 acres of land, and has designated 188 management areas (101 as Wildlife Areas and 87 as Ecological Reserves). A total of 9052 acres is managed specifically for native or rare plant populations and their habitats, primarily on 14 Ecological Reserves.

Because of funding and staffing constraints, the Department's knowledge regarding the presence and status of rare, threatened and endangered plants on its lands is very limited. Most Department lands have not been thoroughly inventoried, and only few priority plant populations are monitored regularly.

HIGHLIGHTS OF CURRENT CONSERVATION ACTIVITIES

Academic researchers throughout California work with the Department under Memoranda of Understanding, Research Permits, and contracts to answer questions that may be important to the conservation of listed plant populations. Some areas of current research include: recovery of *Amsinckia grandiflora*, the role of hybridization for the newly described *Ceanothus ophiochilus*, investigation of the differences in pollinator visitation and seed set be-

tween natural vernal pools and artificially created pools, exploration of evolutionary relationships for *Arctostaphylos* species, and host-pathogen interactions for *Erysimum menziesii*.

The Department co-sponsored a symposium on Monterey pine forest, habitat for at least ten endemic plant taxa including four State-listed species. The symposium was attended by city, county, and state agency personnel, consultants, and local citizens who are concerned about both the loss of forest habitat and the loss of genetic diversity in Monterey pine, an important economic species worldwide. The symposium represented a first step toward recognition of the value of the resource, the threats facing it, and the critical need for regional planning.

Multispecies planning efforts involving threatened and endangered plants are underway throughout California, including western El Dorado County, Sonoma County's Santa Rosa Plains, San Luis Obispo's Morro Bay region, Monterey Pine forest, the Southern San Joaquin Valley, the Owens Valley, and the western Mojave Desert.

The Endangered Plant Program is conducting interagency recovery workshops to identify management and recovery priorities for State-listed plants and to identify funding sources to carry out needed research and on-the-ground efforts. To date, recovery workshops have been held for *Acanthomintha ilicifolia*, *Allium munzii*, *Dodecahema leptoceras*, *Hemizonia conjugens*, and *Holocarpha macradenia*.

Since 1989, the Fish and Game Commission has added 28 plants to the State list of threatened or endangered plants. Only seven of these have been added since 1990. Increasingly, controversy has surrounded each listing petition. This has led to the need for staff to more thoroughly document and communicate information and actions associated with listing.

The Natural Diversity Data Base (NDDB) is converting to ARC/INFO, a commercially available software suite, that will make NDDB's information on California's sensitive plants, animals and natural communities more accessible to its users, which include state and federal agencies, consultants, local planning departments, and researchers. RareFind, the Department's pc-based software application compiled under FoxPro, is currently being improved to give users greater flexibility in searching the database and in creating reports.

(Received 7 Oct 1994; accepted 20 Jan 1995)

PANEL DISCUSSION THE FUTURE OF CALIFORNIA'S FLORISTIC HERITAGE ON PUBLIC LANDS

The future of California's floristic heritage is entwined with the future of its public lands. Approximately half of California, 50 million acres, is public land. The federal government administers 92 percent of these public lands. The USDA-Forest Service (20 million acres), Bureau of Land Management (17 million acres) and the National Park Service (nearly 5 million acres) are the largest federal landowners in California. State government manages 5 percent of the public land and local governments manage 3 percent. Some plant species and communities are restricted to one agency's jurisdiction, while many others occur across agency boundaries. Coordination between government agencies is critical for successful plant conservation. These government agencies need public support to effectively protect, restore and manage plant habitats.

A panel of botanists and biologists from key regulatory and land managing agencies assembled at the Jepson Symposium, to discuss the challenges that government agencies are facing and the role of concerned citizens in influencing the future of California's public lands.

Moderator: Ken Berg, Bureau of Land Management

Panel members: Sarah Allen, National Park Service; Jan Knight, US Fish and Wildlife Service; Sandra Morey, California Department of Fish and Game; Jim Shevock, USDA Forest Service; John Willoughby, Bureau of Land Management

BERG: "California has a history of boom-and-bust economic cycles. For the last few years, the state has been in an economic recession. What should California plant conservationists be doing now, to prepare for future human population growth?"

WILLOUGHBY: "In responding to this question I'll focus most of my attention on the conservation of rare plants. Conserving plant communities, however, is equally important. Many of the points I make relative to rare plant conservation apply equally to plant community conservation. I'll conclude with a few comments on plant communities.

"There are three basic things we need to do, and as quickly as possible: 1) we need to identify those rare plants most likely to be threatened by the increased pressures that will come from human

population increases; 2) we need to identify the occurrences that are most important to these species' viability (a greatly overused term); and 3) we need to preserve the habitats at all these occurrences in perpetuity. We also need to take a fourth action, one that is equal in importance to the others but is too often given short shrift: we need to monitor the populations and habitat we are conserving to ensure our conservation objectives are being met.

"None of this, of course, is new to any of us. We've all been involved in identifying plants that are threatened and endangered for a long time. The California Native Plant Society recently published its fifth edition of the *Inventory of Rare and Endangered Vascular Plants of California* (the first edition was published in 1974). The California Natural Diversity Base has been tracking most of the State's rare plants since the late 1970's and Federal and State agencies have also been involved in this effort at least since the 1970's.

"I maintain, however, that we haven't done a good enough job. That's certainly true for my agency, I suspect it's true for other public lands, and I know it's true for private lands. The information base is definitely better than it was in 1974, when the first edition of the CNPS *Inventory* was published. But it is not even close to being adequate to make the kind of tradeoffs that future land management (and I'm speaking here of management of all lands, including private) will likely require.

"Let me give you an example involving some plants I'm familiar with. A few years ago the Fish and Wildlife Service became concerned that several plant species in the San Joaquin Valley were heading toward extinction. In order to better determine this they let a very modest study to determine the status of these species. The contractor looked at all the herbarium specimens that could be found for these species. All of these documented collection sites were visited (or at least approximately visited) and an assessment made of the habitat integrity at each site. Because the lion's share of these historic sites were no longer considered habitat for the species, the contractor and the Fish and Wildlife Service determined that the species were severely threatened.

"As a result of this study, in June 1990 four San Joaquin Valley plant species were listed as endangered species: *Caulanthus californicus* (Wats.) Pays., *Lembertia congdonii* (Gray) Greene, *Eremalche kernensis* C.B. Wolf, and *Eriastrum hooveri* (Jeps.) Mason. At the time of listing, BLM had very little knowledge of any of these species. Shortly after listing, BLM decided it had better find something out above the species. BLM is responsible for issuing oil and gas leases within the habitat of these species and administers many livestock grazing leases in the area as well.

"In the years since 1990, concerted inventory efforts on the part

of BLM have documented significant new occurrences of two of the listed species—627 new occurrences of *Eriastrum hooveri* and 535 new occurrences of *Lembertia congdonii*, all on public lands. We believe the need for at least *Eriastrum hooveri* to continue to be listed has been called into question.

“Now, I’m not giving this example to criticize the contractor for the study that was done—the study was entirely appropriate and the amount of work done to gather the information contained in the contractor’s report went far beyond what one would expect from the amount of money expended on the study. Nor am I criticizing the Fish and Wildlife Service for listing these two species. That agency is required to act on the best scientific data available, and the best scientific data at the time indicated the species should be listed and listed soon. Rather, I use this example to highlight the fact that we know very little about many of our rare plant species.

“We need to spend a lot more time and effort in inventorying our lands. The BLM waited until the species were listed to gather the information it should have had years before, but, because of budget restraints and other priorities, my agency simply did not collect the necessary data.

“If we don’t have adequate knowledge of the distribution and status of our plant species, we’re going to make a lot of mistakes. And mistakes are not good. Even if we err on the side of the species, we’re going to lose a lot of credibility if we do this very often. This is especially critical on private lands.

“Though our information base is bad on public lands, it is even worse on private lands. Most of our information on private lands, and probably the majority of it on public lands, comes as a result of conducting surveys in conjunction with the preparation of environmental documents. While this information is valuable, it is far from complete. On public lands we spend a lot of time in clearing parcels for projects. What we learn in most cases is negative information—we learn where the species isn’t, not where it is. (Exceptions to this are long, linear projects—e.g., pipelines, transmission corridors—which tend to function as long transects through large areas and yield a lot of information when they cross areas that have not been botanized).

“Proactive inventories, focused on individual species or large areas, yield much more valuable information concerning the distribution, abundance, and status of plant species. These types of inventories, which the BLM has conducted since 1990 on the public lands of the San Joaquin Valley, are almost nonexistent on private lands. Somehow we need to figure out ways of conducting such proactive inventories on private lands. It won’t be easy in today’s political climate, but we must make the effort by working with counties and cities in a nonthreatening manner.

"Inventory will help us decide what occurrences are most important, but this will not be enough. In many cases we will be forced to guess as to how many occurrences are enough, how large they should be, and where they should be. Demographic studies—for those species that lend themselves to these types of studies—will be required for some species. These studies will not determine true "viability" thresholds for such species—for I'm not convinced that's achievable—but they will at least enable us to make more educated guesses as to the appropriate size, location, and number of occurrences necessary to sustain the species.

"Once we have identified those occurrences that are most important, we then must assess the likelihood that these occurrences will persist under present and future management. A gap analysis, similar in many ways to what Frank Davis and others at UC Santa Barbara are involved in for terrestrial vertebrates, will be required for plants. The Natural Heritage Division of the California Department of Fish and Game has made a significant start in this, but is hampered by the lack of inventory information noted above.

"Once we determine the occurrences in need of protection, we must find ways of preserving these areas. Protection doesn't necessarily mean fencing out all human activities and leaving an area alone. Active management will be required in many cases to mimic the types of natural processes under which the target species thrive.

"Those agencies responsible for natural land management must stop being parochial in their management. Ecosystem management and the conservation of biological diversity require that we plan based on ecosystem boundaries—this means we need to work with counties and cities and find ways of protecting species on private as well as public lands.

"Monitoring of those areas managed to conserve rare plants is critical to determine whether conservation objectives are being achieved. This monitoring may be qualitative or quantitative—both types are appropriate depending on individual situations—but it must be done on a continuing basis. Regardless of what we would like to believe, the actions we prescribe to conserve plant species will often fail; we need to recognize (early) when this is occurring and change our management prescriptions accordingly. We can't do this without monitoring.

"The same kind of needs exist for plant communities as for rare plants. The problem is we haven't been spending nearly enough effort on the identification and protection of rare—as well as good expressions of common—plant communities as we have on rare plants.

"Part of the reason for this is there is no law requiring the conservation of plant communities. Another problem is that plant communities are more of an abstract concept than are species, and there is often disagreement over plant community classification schemes

(it is the lumpers-and-splitters argument common in taxonomy taken to a higher power). But there is hope on the horizon. Several agencies have adopted the community classification scheme of Holland (1986), at least on an interim basis, and the California Native Plant Society has recently issued a draft document entitled *Series Descriptions of California Vegetation* (Sawyer 1994). We need to support the work that has been done and to continue our efforts in conserving the vegetation diversity that is so important to California."

MOREY: "One of the most critical issues facing California plant conservationists now is the proposed amendment of the California Endangered Species Act. Several pieces of legislation have been proposed which will change the ways plants are protected, how land use planning will work, who will be making important decisions, and where money will be spent. Business and industry coalitions are very organized and informed, and are calling for major changes in CESA, some of which would drastically weaken plant protection. It is critical for plant conservationists to be informed and vocal, and to fight for amendments which will strengthen our ability to conserve plants. Conservationists must be strongly heard now, especially in the State's current political climate."

SHEVOCK: "Clearly the conservation strategies of the past as viewed by single land use allocations (such as preserves, wilderness, etc.) will have limited success in the future. First of all, we are running out of acres where single land use allocations are available. Acquisition costs per acre may also restrict this type of activity. Regardless of how the land is acquired, one still has to provide for its long-term management, and humans are part of that equation. We as conservation biologists need to assist in creating a conservation ethic in California where humans have a meaningful and tangible relationship to their environment, they understand the need to conserve resources, and actively participate in the process.

"As I look out over the audience in this session, we clearly do not represent a cross-section of the diversity of California. Scotland perhaps but not California! The 1990 census already reflects a large shift in demographics and increases in persons of color as a majority in the near future.

"Are Californians going to vote for conservation based initiatives and ballot propositions if they lack the reasons why conservation is important to the state and their quality of life or for future generations? Why has the conservation/environmental movement not attracted persons of color in any meaningful way?

"Somehow, we as concerned resource professionals have to develop a process to involve other cultures, be completely inclusive, and form new partnerships. Obviously, a lot more than biology is involved in conservation.

"Education and awareness are needed at every level to develop a conservation ethic, one where economic models or short-term profits are not the only driving force in our decision-making process. Conservation will be successful and sustainable when we integrate people as part of the ecological system rather than trying to remove them from it."

KNIGHT: "Plant conservationists can be thinking and working in both the short and long term. To deal with inevitable growth in the short term, conservationists can support California Native Plant Society chapter involvement in local land use planning issues and advocate habitat- or ecosystem-based planning for biological resources, whenever possible. Local planning agencies give varying degrees of attention to rare plant resources in land use plan development. Once general plans are in place, it is difficult to obtain protection for large habitat areas for plants.

"We continually find ourselves in the situation of project by project mitigation under the California Environmental Quality Act or the federal Endangered Species Act, with no mechanism to step back and look at regional conservation strategies that would be ecologically more desirable. Over time, I suspect that many rare plant populations will suffer from this approach, even though they have been "protected" from outright project impacts.

"Also, plant conservationists can look for and develop stronger ties with non-traditional allies such as the livestock industry. Livestock use under informed management may be compatible with recovery needs of many rare plants. Much of the remaining wildlands of the foothills and lower elevations is privately-owned rangeland that is under increasing development pressure. A real opportunity exists for productive partnerships between conservation groups and the ranching community that owns significant habitat for a number of rare plants.

"In the long-term, conservationists can work to instill conservation as a value and priority in younger generations. We all need to do what we can to develop a stronger societal appreciation and awareness for the relationships between standard of living/life-style choices, population growth, and our natural resources."

ALLEN: "There are several things individuals can do, from public service to personal decisions: 1) Contribute to and support family planning groups that advocate zero population growth; 2) support agencies and groups to protect lands from development so that there are corridors between large protected lands; 3) educate our children today so that they will be decision makers of the future with the skills needed to preserve, protect, and restore natural resources."

BERG: "These are difficult fiscal times for public agencies. Budgets and staffing are declining. It is extremely challenging for the agencies

to effectively manage the land with increasing population pressures. What are the three most important things plant lovers can do to help your agency do a better job of conserving native plant habitats?"

SHEVOCK: "The first item is to inform agency administrators of the unique resources that they are to manage for the American people by providing new and/or timely information as it becomes available. Forest Service managers need to have access to the most recent scientific information. Managers also need to be reminded from time to time of the wealth of biodiversity on the national forests and grasslands by members of the public.

"The second item is to be involved. Yes, I know we all hear it, but it really works. If it were not for the efforts of the California Native Plant Society to raise botanical issues to the Forest Service during our land management planning efforts, it is my opinion that our plant program would not have as many full-time professional botanists on staff nor would we have established nearly 75 botanical areas on the National Forests in California or be viewed as a leader in federal rare plant management and conservation.

"The third item is to thank land managers when they do actions that conserve species and their habitats. Being a squeaky wheel gets initial attention, then it's important to follow-up with professional contacts and continued correspondence by building partnerships."

ALLEN: "Develop ties with your congressional (state and federal) representatives in order to develop programs to support the professionalization of National Park Service employees so that more botanists can be hired. Let them know that you care about National Parks in your area. Get involved in regional councils in California where cooperative planning between agencies, businesses, and private individuals for protection of landscapes is going on now. Volunteer for plant restoration programs in a park near you."

MOREY: "Be a vocal constituency. Sometimes decisions are made based on who speaks the loudest. We should broaden our plant conservation constituency with untapped sources of support. Public polls say the number one leisure activity is gardening and that the public believes protecting the environment is important. Maybe we can join forces with groups such as the Nurseryman's Association, or begin to work with our traditional enemies such as the Cattleman's Association.

"The academic community can focus research on questions that will help us more effectively protect and manage plant populations and habitats. We need academic experts to act as our advisors to guide our work and strengthen our positions with scientific documentation. We also need expert testimony in public forums such as at Fish and Game Commission meetings. The testimony of a whole

host of prominent scientists, for example, was very important in our efforts to list the Vail Lake ceanothus as an endangered species.

"Get involved in local land use issues and participate in local conservation planning groups. Share local knowledge of plants, animals, and communities, serve on scientific advisory groups and biodiversity councils."

KNIGHT: "One area in which non-agency plant advocates already are invaluable and that always will be important for this agency, is information. The agency does not have the resources to determine the status and distribution, local threats, and keep up with other local issues that affect all of the candidate plant taxa in California. We rely on grassroots contacts for these kinds of information for many species. We are much more effective within our regulatory scope when we have knowledgeable and reliable local contacts.

"Another way in which non-agency plant advocates can help the Service do a better job of conserving native plant habitats is by providing a strong voice in land use planning and other conservation issues at the local, state, and national level. Local politicians need to hear often and adamantly that rare plant habitat conservation should be implemented in local land use decisions. As I mentioned above, support of a conservation organization in which plants are a conservation priority, such as CNPS, can be effective. An example of a significant national issue for this agency is Endangered Species Act (ESA) reauthorization. Anti-ESA forces that wish to take the teeth out of the ESA in the guise of "improving" it are stronger than ever. All-out effort from the conservation community will be needed to maintain existing ESA protections.

"A third area in which non-agency plant advocates can assist the Service in conserving native plant habitats is developing the non-traditional alliances mentioned above that further the long-term goals of rare plant conservation. Partnerships with owners of some of the best or, in some cases, only remaining native habitat, seems to me to be something that needs to be seriously pursued to complete the overall conservation picture. In California, it is evident that resource agencies never will have the financial resources to purchase and then manage enough habitat that needs protection. Private non-profit organizations cannot provide this function either. The conservation community can develop ways to find and work with receptive landowners to achieve conservation objectives while the land is used also for other purposes, and for economic return. New economic and regulatory incentives could increase the number of receptive landowners, and more probably are needed than exist now before this approach could really be effective."

WILLOUGHBY: "Plant lovers need to work more closely with their local agencies and let their concerns be known. It's not for no reason

that agencies have tended to give more attention (in terms of both money and work effort) to charismatic megafauna and species that are, in the words of a eminent official of the California Department of Fish and Game (who also recognizes this problem), "shot or drug around by the lips." These species have very prominent and vocal constituencies. Those of us interested in plant conservation must take lessons from effective interest groups such as Ducks Unlimited and the American Fisheries Society.

"Plant lovers need to let those in charge of land management agencies know they are very concerned about the plants that occur on the public lands. They should let agencies know of problem situations in a constructive and positive manner.

"When an agency has a success story, recognize it—publish it in newsletters, let the manager and staff know you're pleased. Likely, more such successes will then follow.

"Plant lovers should offer volunteer work parties to assist agencies in special projects, such as restoration work and inventories of specific areas or for particular species.

"Plant lovers should let their elected representatives know about their concerns. Many of you would be surprised at the hoops bureaucrats have to jump through when they get a letter from a Congressman or State legislator. If there are enough hoops, pretty soon the bureaucrat will get tired of jumping and figure out a way of eliminating them—such as by conserving the plant species."

QUESTION #3:

BERG: "American society has very high expectations of its leaders. But we live in a large and complex country and government agencies are unwieldy bureaucracies. The influence of any one person, regardless of job title, is limited in a large agency like the Forest Service, which has 30,000 employees. If you could be Director/Chief of your agency for a day and make 2 proclamations, what would they be?"

ALLEN: "IT'S PLANTS, STUPID. Remember always the NPS adage: 'know, restore, maintain and protect.' "

KNIGHT: "After proclaiming that I would continue indefinitely as Director, I would work with programs on lands owned and managed by the Fish and Wildlife Service.

"I would modify priorities and program emphasis to ensure that the agency's own lands are managed for all biological resources, even if it means less than optimum or otherwise desired production of wildlife resources for which these lands normally are managed. Each refuge has its own purpose and a highly individual program, and authorities and policies would need to be dealt with.

"Determining the status of all sensitive species, including rare plants, on Service lands would become a high priority. The habitat

and other ecological needs of these species then would be identified and integrated into refuge management strategies. The Service should set an example for enlightened ecosystem management for other land management agencies."

MOREY: "I would proclaim that plants will no longer be treated as second class citizens. Currently less than 1 percent of Department of Fish and Game staff positions are botanists. I would begin using our lists of qualified applicants to put staff with botanical/plant ecology expertise in areas where they are critically needed. I would also institute an internal training program for all levels in the Department to increase awareness/knowledge of/appreciation for plants and plant conservation issues so that we would have a bigger and stronger work force actively fighting to conserve and protect our flora.

"I would change the name of the Department of Fish and Game. This visible change would reflect and facilitate the change in the Department's emphasis beyond the traditional game focus to encompass its broader focus of ecosystem and biodiversity conservation."

SHEVOCK: "It is so compelling to ask for more money to increase plant conservation and for hiring additional botanists, but I'd refrain from making those kind of "wish list" proclamations. Rather, I'd focus on proclamations that address fundamental land resource ethics and behaviors.

"I would make a proclamation that reinforces our current agency *Mission, Vision, and Guiding Principles* and highlight sensitive plant (and animal) species as the rarest of the natural renewable resources under our charge. I would proclaim that these species and their habitats are the foundation of ecosystem management and that they are not to be viewed as constraints to other resource programs."

WILLOUGHBY: "My first proclamation would be that I could make an unlimited number of proclamations. However, since neither Aladdin's genie nor you will let me get away with this I'll settle for the following two proclamations: 1. Commodity uses of public land resources will be authorized only after we are sure the native ecosystem will be sustained. This is actually very similar to directives that have already come down from BLM's Director: to manage on an ecosystem basis, to preserve biological diversity, and to ensure sustainable development. 2. If, because of limited personnel and funding, we can't assess, through monitoring, whether our management is in fact achieving our objectives, then we should either not authorize any commodity use at all, or we should authorize it at such a minimal level we can be reasonably sure it is not impacting biological diversity nor threatening the sustainability of ecosystems.

"Proclamations, of course, are the easy part (particularly since everyone knows I'm only going to be in charge for a day). Implementation of proclamations requires the buy-in and commitment of local managers and staff, as well as the public.

"Agencies are notoriously slow in recognizing changing public values. I think the current emphasis placed on ecosystem management by the BLM, the Forest Service, and other agencies is a response by these agencies to changes in public values that began to take place a decade or more ago. The changes required for true ecosystem management to take place are not easy for these agencies to make, and it is unreasonable to expect all agency employees to support them, at least at first. Nevertheless, the changes are coming, and most employees will, in time, support them."

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(Received 7 Oct 1994; accepted 20 Jan 1995)

THE NORTH COAST BIODIVERSITY ARENA IN CENTRAL CALIFORNIA: A NEW SCENARIO FOR RESEARCH AND TEACHING PROCESSES OF EVOLUTION

G. LEDYARD STEBBINS

Section of Evolution and Ecology, Division of Biological Sciences,
University of California, Davis, California 95616-8537

G. FREDERIC HRUSA

John M. Tucker Herbarium, Section of Plant Biology,
Division of Biological Sciences, University of California,
Davis, California 95616-8537

ABSTRACT

The factors responsible for variation in evolutionary rate and pattern among related plant taxa remain in large part obscure. Neutral or selectionist theories alone cannot account for divergent rates of morphological and molecular evolution among related lineages. Interactions among population histories, inherent genetic capacities and environment influence divergence rate. The development of a concise modern evolutionary synthesis, incorporating molecular data and transcending the neo-Darwinian synthesis, is complicated by interaction of these highly complex variables. Control or limitation of these variables is necessary if further evolutionary research is to result in a new synthesis. To this end a biogeographic region is delimited within north-central coastal California and termed the 'North Coast Biodiversity Arena' (NCBDA). The NCBDA has a relatively well-understood geological and environmental history. It is a region of marked microclimatic and edaphic discontinuities, but not one of extreme environments. In general, the climate displays a gradient of decreasing precipitation west to east with simultaneously decreasing equability. It is restricted by definition to elevations below 500 meters. Without high mountain ranges within its boundaries killing frost is essentially unknown. Its topography is varied and in some areas rain shadows have strong local effects. The NCBDA supports a highly diverse flora including both habitat specialists and broadly adapted species. The diversity of major vegetation types, floristic associations, edaphics, and geologies within the NCBDA is introduced. Evolutionary problems critical to the development of a modern evolutionary synthesis and whose solutions may be accessible within the NCBDA are described.

In the mid-1930's, biologists seeking to explain the causes of evolution had reached a point comparable to that which they face at present with respect to the question "Where do we go from here?" Theodosius Dobzhansky provided the stimulus for biologists of different disciplines to combine in constructing the twentieth century (neo-Darwinian) theory by publishing his book, "Genetics and the Origin of Species" (1937). Relevant facts and accessory theories were provided by Julian Huxley in natural history, Sewall Wright and

Ronald A. Fisher in population genetics, Ernst Mayr in animal systematics, G.G. Simpson in paleontology, Bernhard Rensch in animal phylogeny and macroevolution, and G. Ledyard Stebbins in plant evolution.

This mid 20th century synthetic theory, in which natural selection was a prominent feature, lasted for thirty years until it was challenged by two new approaches, one theoretical and the other based upon new facts and techniques. Calculations by Zuckerkandl and Pauling (1962) led to the concept of regular and constant rates of evolution—the Evolutionary Clock. Such a clock would be independent of Darwinian natural selection. If its action were based upon internal, genetically determined factors, regardless of environmental factors, it would relegate the Darwinian concept of evolution to a minor status. Almost contemporaneously, Kimura (1964, 1968) based on his concept of population dynamics, maintained that at the molecular level mutations are neutral with respect to adaptation and so selection must be of minor importance in evolution. Almost immediately after Kimura's first exposition of his neutral theory, Harris (1966) dealing with humans and Lewontin and Hubby (1966) in populations of *Drosophila*, revealed the presence of enzyme differences between and enzyme polymorphism within populations at gene loci that have no obvious effect on adaptation or fitness. Shortly afterward, Kahler and Allard (1970) found a similar situation in plant populations.

The violent controversy that arose from these attacks on Darwinian natural selection raged for twenty years without a consensus and is just now simmering down. Although differences exist among modern evolutionists, neither the extreme view taken by Kimura and early followers of Zuckerkandl and Pauling, nor the prevailing viewpoint of the mid-twentieth century synthetic theory that minimized the importance of neutral mutations, is currently held by modern synthetic evolutionists. The issue between selection and chance is not plus or minus, but one of degree.

As opposed to the 1930's, during the 1990's zoologists and botanists alike are leading the way to a new synthesis incorporating new discoveries this time based upon processes at the molecular level. The recent review of both facts and theories by John Avise (1993) should be studied by all modern synthetists as carefully as was Dobzhansky's review by their predecessors. Although Avise emphasizes metazoan examples, he does include careful accounts of examples from plants.

Most important, his synthesis reflects the demonstration by Watson and Crick (1953), that point mutations are errors in copying. Hence they can be expected to occur much more often than was believed possible before 1950, when mutations were believed to be reorganizations of complex protein molecules (Schrodinger 1944).

Although Gillespie (1991) has provided stimulating material based upon both theory and calculations suggesting that mutations effecting amino acid sequence substitutions in proteins may not be neutral; high frequencies of neutral mutations, if they do exist, are not incompatible with molecular theory which postulates that adaptively significant mutations occur at frequencies high enough to explain the origin of races and species.

With reference to plant evolution, a line of evidence that has developed during the past thirty years indicates that many modern species of woody angiosperms, which have a better fossil record than herbs, have remained morphologically constant for millions of years (Axelrod 1975, 1979, 1985, 1992). Much evidence supports a general combination of the older idea of slow or static evolution, or bradytely, punctuated with much more rapid evolution, or tachytely (Simpson 1944, 1953). Modern evolutionists have largely supported this concept of episodic evolution, or punctuated equilibria (Eldredge and Gould 1972).

A further development from these new discoveries and theories is that rates of phenotype evolution with respect to diagnostic characters of form may or may not agree with rates of biochemical evolution based directly on mutations. Leslie Gottlieb's research on *Clarkia* has shown that in some evolutionary lineages (e.g., *Clarkia biloba-lingulata*) (Gottlieb 1974) morphological and cytological differences are greater than biochemical differences. In other lineages (e.g., *Clarkia rubicunda-franciscana*; Gottlieb 1973) biochemical differences are accompanied by essentially no change in form. Since information obtained from a single genus is subject to so many difficulties of extrapolation from one genus to another, results obtained before the availability of molecular methods cannot be applied to a new synthesis embodying molecular data unless the groups are reinvestigated using molecular methods. Further complicating the development of a new synthesis is the fact that different kinds of adaptive differences may be controlled by different kinds of gene systems. For instance, Clausen and Hiesey (1958) after analyzing covariation of vegetative and reproductive characters among more than 550 F₂ progeny of artificial hybrids between high elevation races and either foothill or coastal races of *Potentilla glandulosa*, found that individual vegetative differences such as overall size, leaf shape and timing and degree of dormancy, are each governed by a larger number of gene loci than are individual reproductive differences such as petal size and color, and seed size. These discrepancies show that new investigations will lead to a new synthesis only if they are designed and conducted in such a way as to reduce to a minimum the number of variations with which one must deal.

The facts reviewed have brought about a dilemma that must be resolved before a new evolutionary synthesis can be constructed. On

the one hand, molecular genetics and developmental physiology favor a clock-like equalization of evolutionary rates. On the other hand, successions of phenotypes through time indicate a highly episodic alternation of rapid and slow rates, the slowest of which amount to evolutionary stasis. In addition, these inequalities of evolutionary rate may affect closely related lineages. Genera with common ancestors such as *Arbutus menziesii* vs. *Arctostaphylos* in the Ericaceae, or *Lithocarpus densiflora* vs. *Quercus* in the Fagaceae display clear differences in rates of differentiation between their respective lineages. On the one hand *Arbutus menziesii* has a fossil record covering 25–30 million years over which little or no morphological change has occurred (Axelrod 1992). On the other hand the closely related and certainly no older genus *Arctostaphylos* has undergone extensive morphological modification resulting in the presence of some 80 more or less well-differentiated forms in California (Wells 1993). Clues to the answer to this question rely upon comparisons between purposeful change produced by animal and plant breeders and the opportunistic changes of which Darwinian evolution consists. Plant and animal breeders have shown that even if directional selection is based upon combinations of mutations each of which by itself has a small effect, they can produce great transformations during periods of time no longer than 100–300 years. Although comparable rates in natural evolution can occur under unusual conditions of strong selection, most evolutionary modifications require tens of thousands or even millions of years. We must conclude that rates of evolutionary change depend not solely upon intrinsic attributes of the organisms themselves, but upon external factors that inhibit or promote the innate capacities of the organisms.

THE VALUE OF SELECTED BIOGEOGRAPHIC REGIONS

Obviously, evolutionists seeking answers to these questions must understand the complexities of the environment with respect to both its present condition and past history just as thoroughly as they must understand the genetic structure and developmental physiology of the organisms that inhabit it. We propose that the most efficient pathway by which a comparable understanding of both organismal and environmental factors within an area may be accomplished is to concentrate upon a natural physiographic and biogeographic region that is so restricted and accessible that it can become well understood. A region so delimited should be one which has a known history of geologic and climatic change during past millions of years, and at the same time contains taxa composed of populations found more or less throughout the region. The region should have general environmental homogeneity except for a limited and comprehensible range of factors. Since any analysis requires alternation between

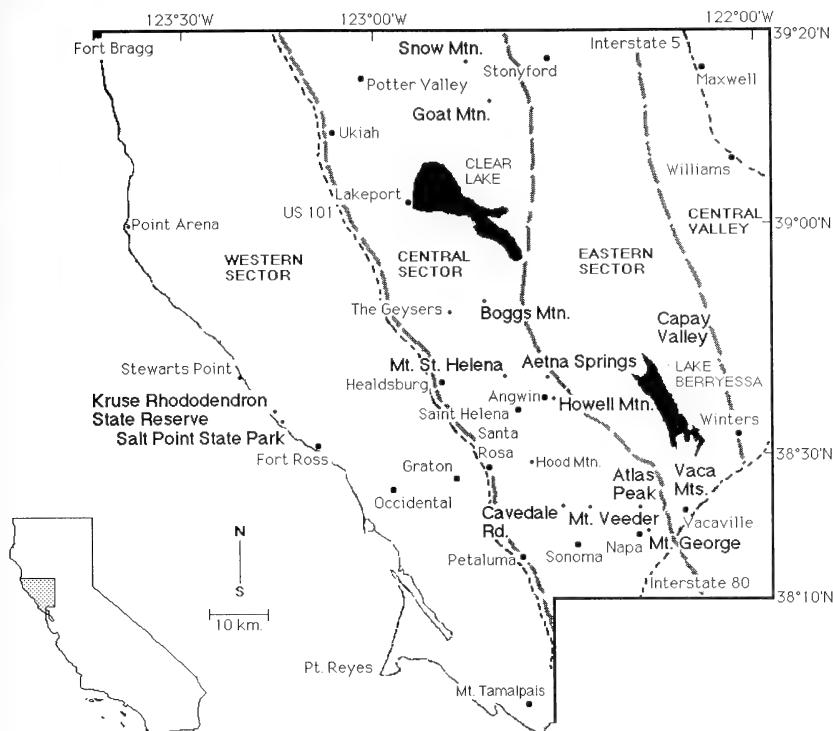


FIG. 1. Map of the North Coast Biodiversity Area in Central California. Geographic features, reserves, parks and cities shown are those discussed in the text, listed in Table 1, or are provided for orientation and clarification.

observations in nature and controlled experiments in the laboratory, the selected region should be easily accessible to well equipped laboratories (see Appendix II).

THE NORTH COAST BIODIVERSITY AREA

These desirable features are characteristic of the region between 38°10' and 39°20' north latitude, extending from the western margin of California's Central Valley, across the North Coast Ranges to the Pacific Ocean (Fig. 1). We propose that this region be designated the North Coast Biodiversity Arena (hereafter referred to as the NCBDA). Because Marin County shares most of the biological and geographical features that make the NCBDA of special interest, it must be included in it as well. Thus, the NCBDA includes all of Marin, Napa, and Sonoma Counties, most of Lake County, the southern portion of Mendocino County and all of western Colusa County. In floristic terminology (Hickman 1993), the NCBDA in-

TABLE 1. MEAN ANNUAL PRECIPITATION AND ANNUAL RANGE OF MEAN TEMPERATURES OF WARMEST AND COLDEST MONTHS AND CALCULATED EQUABILITY M (SEE AXELROD 1967 p. 7) FOR SELECTED SITES WITHIN THE NCBDA. Dashes indicate unavailable site data. See Figure 1 and text for sector delimitation and Figure 1 for site location.

Site	NCBDA sector	Annual precipitation (mm)	Range of means/ Equability (M)
Fort Bragg	western	1013	5.6°C/M 72
Fort Ross	western	1030	5.3°C/M 74
Graton	western	1043	11.3°C/M 64
Occidental	western	1366	—
Point Arena	western	—	5.4°C/M 73
Angwin	central	1028	15.7°C/M 59
Healdsburg	central	1074	13.2°C/M 59
Lakeport	central	759	17.3°C/M 55
Napa	central	630	11.1°C/M 64
Petaluma	central	627	11.2°C/M 63
Potter Valley	central	1153	15.8°C/M 57
Saint Helena	central	899	13.8°C/M 61
Santa Rosa	central	780	11.6°C/M 63
Sonoma	central	715	12.8°C/M 60
Ukiah	central	999	15.4°C/M 58
Stonyford	eastern	505	19.3°C/M 53
Winters	eastern	524	18.0°C/M 53
Lake Berryessa	eastern	—	17.4°C/M 53
Vacaville	eastern	649	16.9°C/M 55

cludes the southern parts of the Inner and Outer North Coast Range subprovinces (NCoRI, NCoRO), and southern North Coast (NCo) subprovince. The present review will describe the ranges of climatic and edaphic variation within this area, the different plant associations that it supports, preliminary notes on these associations that include *Sequoia sempervirens*, and a discussion of specific taxa which present evolutionary problems appearing particularly suitable for investigation within the NCBDA. Throughout the following discussion nomenclature follows Hickman (1993) except where specifically stated.

The NCBDA is divisible into three longitudinal sectors, as illustrated in Figure 1. Among them, the sectors differ in climate (Table 1) and relative frequency of different plant associations. The eastern sector extends from the NCBDA margin near Vacaville, Winters and Williams to the divide between the Putah Creek drainage and the Napa Valley, extending northward to near Stonyford in Colusa County. This eastern sector is devoid of summer fog and subject to high summer temperatures. Its forest associations are confined to oak woodland (*Quercus wislizenii*, *Quercus kelloggii*) and savanna

(*Quercus douglasii*, *Quercus lobata*) with several stands of *Cupressus sargentii* (Sargent cypress) near the western boundary. This sector is the southern part of the Inner North Coast Range (NCoRI) floristic subprovince.

The central sector includes the Napa and Sonoma Valleys, the intervening Hood Mtn.-Mt. Veeder ridge, the Mayacmas Range, and the rugged hilly region north of Clear Lake. The western limit of the central sector lies roughly near US highway 101 (see Fig. 1). Although the central sector peaks and ridges are mostly lower and drier than the Coast Ranges to the north, the rough topography, varied parent materials and diverse soils nevertheless enable this sector to support a highly diverse and discontinuous flora with numerous examples of different plant associations in proximity. Both mean annual precipitation and temperature extremes are intermediate between eastern and western sector values (Table 1). Except for the strictly coastal *Pinus muricata* (bishop pine), all of the tree species occurring in the entire NCBDA are represented in the central sector; only *Pinus ponderosa* (ponderosa pine) and *Calocedrus decurrens* (incense cedar), both highly localized within the NCBDA, are restricted to it. Obviously, the intermediate ecological status and wealth of restricted habitats found within the central sector make it the most likely region to contain interesting examples that shed light upon both the causes of endemism and the ecological factors that affect speciation.

The western sector is dominated by climax redwood forest and the mixed evergreen associations (*sensu* Munz and Keck 1949, 1950); these merge along the sector's relatively sunny eastern boundary. A strictly coastal association, dominated by *Pinus muricata*, separates the redwood association from the actual coast except within a few sheltered canyons where redwoods approach the ocean margin.

Confined in the NCBDA to the western sector are several herbaceous and shrubby species such as western burningbush *Euonymus occidentalis* (western burningbush), *Scoliopus bigelovii* (slink-pod), *Clintonia andrewsiana* (red clintonia), *Vancouveria planipetala* (inside-out flower), *Hierochloë occidentalis* (sweet grass), and *Vaccinium parvifolium* (red huckleberry), all regarded by California botanists as typical of redwood forests, but equally well known to botanists familiar with Oregon and Washington as growing beneath *Pseudotsuga menziesii* (Douglas fir), *Tsuga heterophylla* (western hemlock) and other conifers.

PRINCIPAL CLIMATIC PARAMETERS OF THE NCBDA

I. Temperature (see Table 1). The NCBDA lies entirely at elevations below 500 meters within central California, and so does not include any areas subject to killing frost or snow; frost prone regions

within its boundaries but theoretically excluded from the NCBDA include the highlands of Mt. St. Helena, Boggs Mountain, Goat Mountain and Snow Mountain, all within the central sector.

The NCBDA is entirely within the summer-dry Mediterranean climate region, suffering most of the warm season without significant precipitation. Drought stress is greatly alleviated in the western sector where almost daily fog keeps the maximum temperatures down to 19°C (66°F) and maintains atmospheric humidity of 50% or higher during the critical middle parts of the day. The sector is also one of mild temperatures with high equability ($M \pm 70$ see Table 1) and a generally low range between means of the warmest and coldest months of the year (Table 1). Central sector temperatures, humidities and equabilities are intermediate and vary greatly between adjoining localities, depending upon features of the rugged topography and their effects on wind direction, whether oceanic or landward. In this central region, adjacent or nearby plant populations may be exposed to very different temperature and moisture regimes, such that cross fertilizing species dependent upon insects and other vectors often will produce progeny that are highly heterozygous for alleles controlling adaptations to tolerance of temperature and moisture stress.

II. Precipitation (see Table 1). Mean annual precipitation values recorded by weather stations along or adjacent to the North Coast Biodiversity Arena (NCBDA) vary from approximately 500 mm (20 inches) at Winters in the Central Valley, to 1030 mm (41 inches) at Fort Ross on the coast, and 1360 mm (54 inches) at Occidental in the western sector redwood forest. Central sector precipitation values are intermediate and highly variable, depending on the presence or absence of the local rain shadows that abound in the rugged terrain.

Nevertheless, even these great differences fall within the tolerance ranges of an unknown but probably fairly high proportion of the species that occur within the NCBDA, since some of them e.g., *Quercus kelloggii* (California black oak), *Mimulus aurantiacus* (sticky monkeyflower), and *Clarkia concinna* (red ribbons) are almost equally common in both the western and eastern sectors. In many instances, differences in edaphic distribution may compensate for climatic differences, so that a population growing in a relatively low moisture region may possess genotypes adapted to shady localities or relatively heavy soils having high water holding capacity, while other populations of the same species may be adapted to moister climates, but to soils with low water retention. Overall a major problem confronting plant ecologists interested in evolution is the presence, absence, frequency and significance of compensating adaptive equilibria. The North Coast Biodiversity Arena provides an ideal scenario for investigating these phenomena.

EDAPHIC DIFFERENCES, REGIONAL AND LOCAL

For two main reasons, the North Coast Biodiversity Arena is particularly valuable for analyzing adaptive plant evolution and speciation. First, the general position of the NCBDA relative to California's gradient climate is intermediate between that of deserts and steppes, and that of dense forests either tropical or temperate. In more arid climates, drier sites have such depauperate plant communities and extreme individual adaptations to aridity that opportunities for comparison of adaptations among the organisms are highly limited. Forests in more mesic climates are generally underlain by soils that have been so much modified by deposition and decay of organic matter that they reflect very poorly differences in parent material and geological history. Within most of the NCBDA, the intermediate climate tends to emphasize differences in soil type, texture, mineral content, and chemical content of parent materials which are often strongly manifest and influence greatly the varied success of competing species. Furthermore, microclimates based upon the rugged topography in combination with strongly manifest edaphic influences, often allow juxtaposition of plant associations and the survival of combinations of plant taxa unusual for central California.

Second, if we consider also the geological time scale and current knowledge and theories about the history of California's landscapes and its flora (Raven and Axelrod 1978; Schaffer 1993; Wilkin 1993), we must appreciate even more highly the value of the NCBDA. From the time when modern angiosperms occupied lands that were to become California, right up to the present, a succession of crustal movements, displacement of mountains, elevation of new mountain ranges, volcanism, and climatic changes, have occurred. These shifting climates and landscapes gave rise both to changes in plant species diversity and in the nature of the transitions between different ecological habitats evident throughout the NCBDA. Three situations are particularly worthy of mention: 1) the transition from grassland or chaparral to oak or mixed evergreen forest; 2) the unpredictable occurrences of species in marginal mixed conifer-redwood associations; and, 3) the often sharp boundary along the coast between mixed conifer-redwood and closed-cone pine forest.

As a background, the topography and geology of the area can be described as follows: On the eastern margin presently uplifted Cretaceous marine strata (120–70 MYBP), were deposited on the shores of the Sacramento Sea, which at that time occupied the present site of the Central Valley. These marine strata alternate between layers of sandstone, composed of coarse sands and gravels deposited during periods of active uplift; and shales, consolidated muds and clays laid down during periods of relative geological quiescence. Within

the NCBDA these formations compose the Vaca Mountains, the ridge between Capay Valley and Lake Berryessa, and the low ranges to the north adjacent to the western margin of the Central Valley. The vegetation and flora occupying these parent materials are those typical of the inner North Coast Ranges and are developed as two major vegetation types: 1) woodlands and savannas dominated by *Quercus wislizenii* (interior live oak), and *Quercus douglasii* (blue oak); and, 2) chaparral composed mostly of *Adenostoma fasciculatum* (chamise) and *Quercus berberidifolia* (scrub oak).

The central and western sectors are underlain chiefly by metamorphic rocks of the Franciscan series, ranging in age from Jurassic to Cretaceous (150–100 MYBP). More recent formations outcrop near the eastern boundary of the central sector, and along the Pacific coast. As regards the former, during the Pliocene epoch (7–3 MYBP) volcanic eruptions partly covered the hills surrounding the Napa and Sonoma valleys of the central sector with lava, volcanic ash, and mudflow breccias. Subsequent tectonic uplift and faulting has created a patchwork of parent materials that now support an equally complex pattern of forest elements. This complex geologic and floristic patterning centers about Howell Mountain, particularly its steep northeast-facing slopes. An ecological analysis of the mixed evergreen forest found in this area should increase greatly our understanding of the mixed evergreen forest type as a whole, at least with reference to its Californian facie. Equally complex geologies and floristic patterns extend to the southwest as far as the Sonoma Valley, and northwest to Mt. St. Helena.

Turning to the western edge of the NCBDA, geologists have recognized its coastal formations from Fort Ross north to Stewarts Point as the northernmost extremity of faulting and movement along the San Andreas fault. West of the fault line itself, in the region of Fort Ross and Salt Point State Parks and the intervening area, coastal vegetation is completely different from that which flourishes less than a kilometer inland (~½ mile), e.g., at Kruse Rhododendron State Reserve. Preliminary evidence based upon soil chemical composition and soil depth suggests that analysis of this area within the NCBDA with reference to these factors, would be most rewarding and may provide clarification of the relative importance of chemical versus physical edaphic conditions as they influence vegetation and floristic patterns.

In the forests of the western sector, high soil and atmospheric moisture combined with relatively equable temperatures promote increased biomass and accumulation of surface litter. The resulting increase in organic content of surface soils promotes the spread of species that are unique to this area within the NCBDA, e.g., *Scoliopus bigelovii*, *Clintonia andrewsiana*, and *Hierochloë occidentalis*.

THE DIVERSITY OF EDAPHIC ISLANDS

In this discussion, edaphic islands are defined as restricted areas distinguished by a soil type or parent material markedly different from that of the surrounding region, supporting one or more highly localized species possibly endemic to the edaphic type. The present area contains three widespread and distinctive kinds of edaphic islands, each of which depends upon a different edaphic characteristic.

1. *Serpentine islands.* Serpentine islands are associated with the Franciscan formation (Jurassic–Cretaceous), and are scattered throughout the area. South of the NCBDA, in the San Francisco Bay Floristic Province (SnFrB), they occur chiefly in association with the San Andreas Fault. North of the San Francisco Bay, including the NCBDA and other areas to the north, particularly the Klamath–Siskiyou region, the serpentine occurs near areas of volcanic activity, and may have been emplaced at the land surface in association with newly forming volcanoes (E. Moores, personal communication).

Serpentine soils are derived by weathering from ferro-magnesium silicate (ultramafic) parent materials. Ultramafic rocks have a relatively high content of iron and magnesium and little or no calcium. Plant endemics that have become adapted to them differ greatly in composition and abundance among the serpentine islands depending on the degree of weathering, the chemical and physical attributes of the serpentinite, and available soil and atmospheric moisture. In general, serpentine islands found in the western sector are relatively small and widely separated, while those in the central and eastern sectors are larger, sometimes merging into each other. These size and distributional differences among the serpentine islands are reflected in the distribution of the endemic plant species. Many of the plants restricted to serpentinite in the western sector are highly restricted, and may be related to serpentine endemics found outside of the NCBDA, while those in the central and eastern sectors are usually more widespread within the NCBDA and have disjunct distributions in different serpentine islands. The most widespread serpentine specialists in and near the NCBDA are *Ceanothus jepsonii* (musk brush), *Cupressus sargentii* (Sargent cypress), *Quercus durata* (leather oak), and *C. macnabiana* (MacNab cypress). The latter pair of species occur also on other kinds of edaphic islands.

Since the NCBDA contains several evolutionary complexes that include a combination of serpentine endemics and closely related species or races that do not grow on serpentine e.g., the *Streptanthus glandulosus* complex (Mayer and Soltis 1994), the area offers unusual opportunities for experimental analysis of genetic characters, particularly those that might increase the fitness of genotypes adapting

to this unusual habitat. Particular attention should be paid to *Ceanothus* subg. *Cerastes*, and *Hesperolinon* in addition to the *Streptanthus* complex mentioned above.

2. Hard rock volcanics. The central sector of the NCBDA is strongly influenced by the Pliocene volcanic activity centered near Howell Mountain. Volcanic activity is manifest in surface geologic formations extending in the south from near the cities of Napa and Sonoma, north to Mount St. Helena. Outpourings of lava and other molten rock hardened into geologic formations that erode very slowly, yielding a very thin soil that becomes saturated during the winter and dries out rapidly during the early spring. Sites with this shallow soil subject to saturation and rapid drying are often dominated by specialized endemics adapted to tolerate these environmentally stressful conditions. Along the east side of the Napa Valley, where the hard rock layers are only slightly tilted, the endemic *Ceanothus purpureus* forms large populations. Elsewhere, particularly along the unnamed ridge north of Mt. George that culminates in Atlas Peak, and along various parts of the Mt. Veeder-Hoods Peak Range to the west a distinctive annual endemic, *Madia nutans*, is adapted to this harsh habitat. Indirect evidence suggests a relatively recent origin for these narrow endemics, but this problem needs to be attacked using molecular techniques, particularly polymerase chain reaction-assisted DNA analyses.

3. Fossilized volcanic ash. Pliocene volcanic activity in the NCBDA distributed mineral ash layers over a wide area. Ash layers that did not become eroded away became embedded with older geologic strata as a result of faulting and uplift. Soils consisting largely of this mineral ash are acidic, low in major nutrients, and produce physiologic stresses unfavorable to the dominant species e.g., *Pseudotsuga menziesii*, *Arbutus menziesii*, and *Quercus kelloggii*. In these highly localized sites, the dominant forest taxa are replaced by stress tolerant species such as *Pinus attenuata* (Knobcone pine), *Arctostaphylos canescens* (hoary manzanita), *A. standfordiana* (Stanford's manzanita), *Xerophyllum tenax* (beargrass), *Salvia sonomensis* (Sonoma sage), and *Cupressus macnabiana*. The best example of a fossilized volcanic ash edaphic island is found along Cavedale Road, Sonoma County, and contains these alternate forest species which among other taxa have entered the edaphic island from various directions and divergent habitats. Representative species at Cavedale which are well-developed in other parts of the North Coast Biodiversity Arena include *Pinus attenuata*, *Arctostaphylos* spp. and *Salvia sonomensis*. Species from more xeric regions include *Cupressus macnabiana* and *Helianthus gracilentus* (slender sunflower). Those species with their best development on more mesic higher mountain slopes include *Xerophyllum tenax* and *Viola lobata* (pine violet). Taxa found mostly in the equable coastal zone to the west

are represented at Cavedale by *Chrysolepis chrysophylla* var. *minor* (dwarf chinquapin) and *Solidago spathulata* (coast goldenrod). The disparity of these sources is clear evidence that the distribution and establishment of these invasive species is independent of surrounding species, and is governed chiefly by the availability of a niche to which they can become adapted.

THE VEGETATION OF THE TRANSECT

Description and characterization of the vegetation within the North Coast Biodiversity Arena is the most difficult section of this review. This is because the literature in ecology has for a century been cluttered with numerous attempts to define a few easily recognizable principles, trends, or categories, none of which has succeeded. This problem has been reviewed in a reasonably successful manner by Barbour et al. (1993), and in a different way by Begon et al. (1986). A further complication is that the recent floristic classification of the area by Hickman (1993) has added the names of floristic provinces and subprovinces that have previously been mentioned, and these must be considered in connection with any proposed classification.

We have already recognized that the NCBDA flora should be included in three floristic subprovinces, North Coast (NCo), North Coast Ranges Outer (NCoRO), and North Coast Ranges Inner (NCoRI). Although the division between the NCoRO and NCoRI is difficult to place physically within the NCBDA, a classification of the vegetation is even less clear-cut, primarily because of the large number of edaphic islands with their unique combinations of flora.

We follow Barbour et al. (1993, pp. 6–7) in recognizing a relatively small number of vegetation types. These are defined chiefly on the basis of climatic and edaphic factors that affect the association of species in a particular area. Thus, we recognize within the area seven vegetation types, as follows: 1) Coast Interface (*sensu* Barbour et al. 1993); 2) Mixed Evergreen Non-Riparian Forest; 3) Mixed Riparian Forest; 4) Single Tree-species Forests/Woodlands individually dominated by: A. *Pinus muricata* B. *Quercus wislizenii*, C. *Cupressus sargentii*, and D. *Pinus attenuata*; 5) Oak-savanna-grasslands; 6) Brushland Communities; and 7) Wetland Communities.

1. *Coast interface.* Edaphic diversity permits recognition of three separate subdivisions: 1) sandy beach and dunes; 2) rocky shore and coastal bluff; 3) coastal scrub and grassland, dominated by *Baccharis pilularis* (coyote brush), both upright and prostrate forms plus intermediates. The subdivisions of this type are united through their direct exposure to winter storms and summer fogs, linear shape several kilometers in length from north to south, and width from

shore to inland mixed forest varying from only a few tens of meters to at most one or two kilometers. Although the great majority of the species included are either widespread along the Pacific Coast or are found chiefly south of the area e.g., *Dudleya farinosa* (rock lettuce), a few are more northern in distribution, e.g., *Polypodium scouleri* (Scouler's polypody). Northward in Mendocino County, the subdivisions assume a more northern aspect, particularly with respect to the conifers that separate the redwood and mixed evergreen forests from the coast itself. There *Picea sitchensis* (Sitka spruce) and *Pinus contorta* (shore pine) may locally replace *Pinus muricata*.

Except for *Baccharis*, the species that make up this vegetation exhibit little relationship to those of the interior vegetational types of the NCBDA, and so are not discussed. On the other hand, *Baccharis pilularis* requires special attention, since it illustrates the principle of edaphic compensation. The upright form of *Baccharis pilularis* is the most common species in the NCBDA that clearly illustrates this principle. At the extreme of the western sector, exposed to the cool foggy climate of the immediate coast, *Baccharis* succeeds best on the warmest driest slopes where soil water retention is low. In Cold Canyon near Monticello Dam at Lake Berryessa in the eastern sector at the opposite edge of the NCBDA, *Baccharis* is a subriparian species that can resist the stress of drought and heat only by growing as near to the stream bed as possible. This principle may be applicable to a large proportion of those species distributed over the entire NCBDA.

The phenomenon of edaphic compensation in *Baccharis* highlights a basic problem of evolutionary genetics in plants. Is compensation achieved by phenotypic modification of one or a few similar genotypes, or is it achieved by mutation, recombination and natural selection involving many genes and gene systems, and accompanied by major processes of directional Darwinian selection? If the latter is true, what is the nature of the gene systems involved, in terms of the developmental-physiological action of their products?

Representing an initial approach to a solution of this problem are the experiments of (Clausen et al. 1940; Clausen and Hiesey 1958). On the basis of their results one can conclude that approximately one-half of the phenotypic differences between *Potentilla glandulosa* from timberline and foothill ecotypes in the Sierra Nevada is based on genetic differences and the other half on phenotypic modification.

A related experiment on *Rhododendron occidentale* (western azalea) backed by molecular data on electrophoretically active enzymes, has shown NCBDA western sector populations differing from eastern sector populations not only with respect to factors probably associated with climatic differences, but also with respect to the abundance and distribution of trichomes that may serve as insect repellents. Moreover, some of the azalea populations, particularly those

located in the eastern sector, grow preferentially on serpentine soil, and have developed adaptations to the stresses that it imposes (Hrusa, ms. in prep.).

2. *Mixed evergreen forest.* Between one-third and one-half of the NCBDA is covered with a forest consisting of conifers, broad-leaved evergreens and broad-leaved deciduous trees, chiefly oak species. Authors have attempted to divide the mixed evergreen forest into communities or sets of communities (Holland 1986; Sawyer et al. 1988), but according to our observations these components blend into each other, except where separated by distance. As clearly recognized by Barbour et al. (1993), the mixed evergreen forest of northwestern California is only a southward extension of the vast holarctic coniferous forest that encircles the northern hemisphere between latitudes 45° and 55° north. Except in coastal California and a few other places, it is dominated in the United States by three widespread species; *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Picea engelmannii* (Engelmann spruce). In Canada it is dominated by species of *Abies* and *Picea*.

There is no doubt that the California version of this forest, on the whole, contains dominant trees that exhibit a range of physiological optima. In rough order of preference for mesic conditions are *Sequoia sempervirens* (coast redwood), *Pseudotsuga menziesii*, then *Lithocarpus densiflora* (tanoak), followed by madrone *Arbutus menziesii* and the subdominants *Quercus garryana* (Oregon oak), *Umbellularia californica* (California bay) and *Quercus kelloggii*. Nevertheless, unless careful comparisons of undershrubs and perennial herbs give support to any classification that might be suggested, we doubt that a subdivision into distinct communities can be realistically maintained. Impressive and distinctive as it appears to be at first sight, we believe that the *Sequoia sempervirens* forest can be recognized only informally as a region of the larger forest area. This opinion is based upon comparisons of forests containing redwood which are found within the NCBDA from near the immediate coastline to the eastern sector's western boundary. These latter redwood groves are the most interior localities known for the species and occur outside regular summer fog cover nearly 60 kilometers from the coast.

Based upon observations in Humboldt County, Barbour et al. (1993) describe a series of climax distributions based on altitude. In our area, however, similar distributions occur in a serial fashion at altitudes less than 450 meters (1500 feet). Therefore the distributions are probably attributable to differences in fog persistence affecting summer temperatures, as well as proximity to streams, microclimatic factors such as slope orientation and specialized edaphic conditions.

3. *Riparian mixed forest.* Since the NCBDA was purposely delimited to avoid the coastal valleys and rivers, it does not include any highly developed riparian forests. The only river that flows through the NCBDA for any distance is the Russian River in the western sector. So far as we know, its riparian forest has not been investigated in detail. In the central sector, the Napa River flows past vineyards for most of its length and has little undisturbed riparian forest, except for a remnant near Yountville managed as a reserve by the California Department of Fish & Game. In the eastern sector lies the drainage of Putah Creek, much of which has been converted by the Monticello Dam into Lake Berryessa. Hence, as compared to other parts of Northern California, the present area is unfavorable for investigating major riparian forests and the species they contain.

Nevertheless, the NCBDA contains a large number of lower order streams, bordered by distinctive species. Several of these are the only species of their genus found in the area, such as *Calycanthus occidentalis* (spicebush), *Cercis occidentalis* (western redbud), *Acer macrophyllum* (big-leaf maple), *Amelanchier alnifolia* (sarvis), *Aralia californica* (elk clover) and *Vitis californica* (wild grape). Because most of these species occur in at least two and often all three sectors of the NCBDA, and except for *Calycanthus*, *Cercis*, and *Amelanchier* belong to genera that have numerous species in other parts of their geographic ranges where they are not strictly riparian, the local evidence supports the possibility that the local mesic riparian environment is not conducive to speciation. This hypothesis is supported by the numbers of species exist, both generally and in the NCBDA, in the two genera of Salicaceae, the most characteristically riparian of northern temperate genera. The genus *Populus*, which is predominantly riparian, contains only about 40 species, while *Salix*, in which several riparian species are accompanied by a larger number that are adapted to meadows, bogs, wet mountainsides and other non-riparian habitats, contains approximately 400 species. The genus *Salix* is well-recognized for its many difficult taxonomic and evolutionary problems, including polyploidy and in the NCBDA, adaptation to serpentine.

Several year-round streams cut through serpentine rock, such as Austin Creek (western sector), Little Stony Creek and Butts Creek (both eastern sector). These serpentine riparian sites support a distinctive flora with many relictual endemics e.g., *Senecio clevelandii* (Cleveland's ragwort) and *Delphinium uliginosum* (bog larkspur), in addition to species disjunct from other regions e.g., *Castilleja miniata* (great red paintbrush) and *Parnassia californica* (grass-of-Parnassus).

4. *Single tree-species forests/woodlands.* In addition to the complex mixed evergreen forest, the NCBDA includes part or all of four

forest types that are each dominated by a different single tree-species. These single tree-species forests/woodlands are each associated with a particular stressful habitat, and may be restricted to a specialized edaphic type.

*A. Bishop pine (*Pinus muricata*) forest.* At the western margin of the NCBDA, on coastal terraces from Fort Ross and Salt Point northward to beyond our area in northern Mendocino County, occurs *Pinus muricata*, a closed-cone pine of southern affinities. In our area the flora associated with *P. muricata* is particularly depauperate. This is due in part to the exposure of the coast to severe winter storms that twist many trees into fantastic shapes beloved by artists (Smith and Wheeler 1990–1991). A suspected but undocumented second factor is shallow soil. In this regard coastal terraces are known for their poorly drained highly podzolized soils on which pygmy forests including bishop pine sometimes occur (Baker 1972) and thus, relatively shallow and impermeable subsoil may contribute to the presence of bishop pine forest in our area.

*B. Knobcone pine (*Pinus attenuata*) forest.* Closely related to the bishop pine, knobcone pine forms nearly pure forests on the ridge between Hood Mountain and Mount Veeder (see Fig. 1). The pines occur in various-sized stands interpolated within the dominant mixed evergreen forest. These stands of *Pinus attenuata* are restricted to the fossilized volcanic ash deposits described previously. Associated plant species range from the diverse flora of mesic and north-facing slopes as described for the Cavedale Road edaphic island to understories restricted to *Arctostaphylos stanfordiana*, *A. canescens* and *A. glandulosa* on dry south to west-facing slopes. In the northern portions of its range *Pinus attenuata* occurs mostly on serpentine (Kruckeberg 1984) and indeed it is found on serpentine in the NCBDA in the northern central sector near the summit of Red Mountain South between Hopland and Ukiah (Smith and Wheeler 1990–1991). *Pinus attenuata* is also found on peaks and higher north-facing slopes in northern Lake County (McCarten 1988), but these and the Mendocino County occurrences on serpentine all appear to exceed the 500 meter elevation limit for the NCBDA. The best developed stands in the NCBDA at elevations below 500 meters occur on volcanic ash in the southern region, where knobcone pine is so tightly adapted to the ash deposits that on sites where ash and serpentine interfinger such as near Aetna Springs above Pope Valley, *Pinus attenuata* avoids the serpentine and occurs only on volcanic ash. The genetic basis for this differential adaptation to serpentine and volcanic ash should be investigated because within the NCBDA these substrata support generally exclusive floras. Among the remaining woody species of the NCBDA *Quercus durata* and *Umbellularia* also occur on

both ash and serpentine. *Quercus durata* attains its best development on serpentine and where it grows on volcanic ash its form tends to vary slightly toward *Q. berberidifolia* which within the NCBDA is found only on unspecialized substrata. The biology of *Umbellularia* is poorly known and essentially nothing can be said regarding the edaphic factors involved in its distribution. Preliminary investigation of morphological variation in *Umbellularia* across edaphic and climatic variables suggests that while racial variation probably does exist, the patterns are complex and in need of further clarification.

*C. Sargent cypress (*Cupressus sargentii*) forest.* The final single tree-species forest to deserve attention is *Cupressus sargentii* which occurs in several large stands on hillsides underlain by serpentine soil. This single tree-species forest deserves attention in the NCBDA because the growth habit of the cypresses may approach that of *Cupressus macnabiana*, although the trees generally have the differentiating characters of *Cupressus sargentii*. Distinguishing *Cupressus sargentii* and *C. macnabiana* in the NCBDA is often highly subjective and an investigation of the patterns of variation among the NCBDA populations of these two cypresses would do much to clarify their overall relationship. A little known stand on the west side of Lake Berryessa is dominated by dwarf trees usually less than 2 meters in height. When explored carefully, this forest may be found to contain serpentine endemic races or species that are as yet unrecognized.

*D. Interior live oak (*Quercus wislizenii*) woodland.* In the eastern sector at the margin of the NCBDA, the slopes of the Vaca Mountains facing the Central Valley contain in protected canyon bottoms and on northeast-facing slopes a forest consisting almost entirely of *Quercus wislizenii* with scattered individuals of *Aesculus californica* (California buckeye). In the more mesic enclaves of this single tree-species woodland the herbaceous flora contains species found throughout the NCBDA, e.g., *Cardamine californica* (milkmaids), *Fritillaria affine* (checker lily), and *Dodecatheon hendersonii* (shooting stars). Drier sites support species of limited distribution within the NCBDA but which extend in range to the Sierra Nevada foothills, e.g., *Chorizanthe membranacea* (pink spineflower), or are disjunct from regions to the south, e.g., *Gutierrezia californica* (snakeweed).

5. Oak savanna-grasslands. The grassland savanna vegetation type within the NCBDA has been so much disturbed during the past 200 years by livestock grazing and introduction of European annuals that evolutionary investigations based on this type will not be sufficiently rewarding to justify the time and money necessary for them.

6. Brushland associations. Investigations of shrubland or chaparral will be most rewarding. Two genera that include the majority of

woody species found in this vegetation type deserve particular attention, *Arctostaphylos* and *Ceanothus*. Of these two, *Arctostaphylos*, although well represented in the NCBDA, is richer in endemic species from the San Francisco Bay Province southward into Baja California. Moreover, it has proved to be difficult in the way of genetic investigations. Although seed germination under artificial conditions has been successful for most species, percentages are too low to enable unbiased progenies to be raised from either artificial or suspected interspecific hybrids or their parents. Although generation by generation analyses of allozyme alleles will partly overcome this defect, it is doubtful that it can be fully overcome.

On the other hand, species and hybrids of *Ceanothus* are routinely grown from seeds in gardens and arboreta (Schopmeyer 1974). Of the two subgenera of *Ceanothus*, *Euceanothus* and *Cerastes*, there are respectively seven and twelve taxa found within the NCBDA. A center of recent speciation in *Cerastes* is in or near the NCBDA, as evidenced by the six narrowly endemic taxa of the total of twelve found there (Schmidt 1993). In contrast there are no endemics among the six species of *Euceanothus* within the NCBDA. Over the range of the entire genus *Ceanothus*, the ratio of narrow endemics to widespread taxa is considerably broader in subgenus *Euceanothus* than in subgenus *Cerastes*. An interesting problem of phytogeography and evolutionary ecology is why this pattern should occur within a single genus.

At the opposite extreme is the most common dominant species of chaparral, *Adenostoma fasciculatum*, which has no living relatives except for its localized congener *A. sparsifolium* (redshanks) of desert margin habitats. Axelrod (personal communication) believes that *Adenostoma* must have originated no more recently than 9–10 million years ago in the Upper Miocene, and in spite of an increase and fluctuations during the subsequent millennia of habitats favorable to it, has not given rise to any derivative taxa, or at least none that are extant. Among the three sectors of the NCBDA *Adenostoma* is found in each on a diversity of substrata and in various exposures. The species is genetically distinctive among habitats in central California (Anderson 1954). Within the NCBDA its pattern of variation across habitats is unknown.

7. *Wetland associations.* Wetland habitats are among the most impacted in California; probably only the annual grasslands are more altered from their pristine state. Throughout the NCBDA there occur many small and large springs, at least one major wetland—Pitkin Marsh—in the western sector, and a remnant set of vernal pools in the vicinity of Santa Rosa, all of which have been severely impacted. There are numerous hot springs concentrated in the volcanic region immediately south of Mt. St. Helena, but most of these have been converted to resort use. Immediately northwest of Mt. St. Helena

occur the endemic taxa *Poa napensis* (Napa bluegrass), and *Dichanthelium lanuginosum* var. *thermale* sensu Spellenberg (Geysers dichanthelium), both of which are restricted to warm, moist, alkaline sites near The Geysers in the Mayacmas Mountains. The wetland habitats within the NCBDA are so altered we feel they are no longer of broad value for evolutionary studies. Ecological questions may be addressed in specific localities, but overall the habitat is relatively unproductive in terms of evolutionary studies at the present time.

ECOLOGICAL STABILITY, CHANGE AND SPECIATION

Previous experience with higher plants, plus observations during the present season within the NCBDA have strengthened our belief that speciation rates measured in terms of established species depend as much or more upon the diversity of the habitat as it affects Darwinian natural selection, than upon genetic processes occurring within individuals and populations. The present section of this review starts with the assumption that this hypothesis is correct, and asks the question: Are the resources of genetic and specific variation among the genera found within the NCBDA great enough, and of such a nature that investigations of its plant populations will lead to a testing of this hypothesis and to a greater understanding of speciation in general?

A review of the genera found within the area shows that among them are at least 22 that present interesting problems. These concern six degrees of divergence. Some levels of divergence remain strictly at the racial level e.g., *Rhododendron occidentale* and *Umbellularia* as discussed previously. The next two defined levels of divergence have biologically imperfectly isolated species-pairs occurring with or without some degree of fidelity to specialized climatic or edaphic situations. The first group includes among others the recognizable species-pairs, *Rhamnus californica/tomentella*, *Monardella viridis/villosa*, and *Delphinium decorum/nudicaule*. The latter pair of species are especially interesting due to their divergent floral forms based upon developmental paedomorphy. In this light the evolution of the narrow endemic *Delphinium luteum* by hybridization of *D. decorum* and *D. nudicaule* (Guerrant 1978) is of special interest. The second group has species that can usually be recognized in nature but among which isolating barriers of a genetic nature are weak or absent e.g., *Rhamnus crocea/ilicifolia* which intergrade across a climatic gradient, *Ceanothus* subg. *Cerastes* discussed in detail in a previous section and whose species tend to display edaphic fidelity, and the genus *Quercus* which across the NCBDA has numerous interesting problems concerning hybridization and introgression. Then come genera within which species are strongly isolated from each other based

upon genetic-developmental barriers that affect growth as in *Linanthus* (*L. bicolor*/cf. *androsaceus*) where different somatic DNA content and differential sensitivity to artificially applied growth substances reflect differences in the natural environment of the species (Stebbins, unpublished data). Finally there are examples of genera that contain strongly isolated subgenera, within each of which isolating barriers are of a different nature (*Madia nutans/rammii* vs. *Madia stebbinsii/hallii*), and at the strictly macroevolutionary level are genera of which the taxonomic position is doubtful (*Calycanthus*, *Umbellularia*) and whose affinities may be revealed by molecular methods.

These examples and others will be discussed in greater detail elsewhere. Here, only two more general points need to be emphasized, although their solutions would benefit by investigation within the NCBDA. First, the preliminary data show that several different patterns of speciation exist, and that their occurrence is independent of the taxonomic position of the entities involved. Three examples show striking differences between closely related genera or subgenera. First, in the Ericaceae, *Arbutus* in California consists of a single homogeneous species that, according to fossil evidence, may be at least 25–30 million years old. The neighboring genus *Arctostaphylos* is certainly no older, but is divisible into an indefinite number of species, ranging 50–80, depending upon taxonomic treatment.

Second, in the Fagaceae, *Lithocarpus densiflora* is a single species that on the basis of fossil evidence including both leaves and acorn cups is at least 40 million years old, while *Quercus* species that either migrated into California or originated there during the past 25–30 million years appear to have given rise to several additional species during the past ten million years.

In the Fabaceae, *Pickeringia* (chaparral pea) and *Thermopsis* (false lupine) both contain only a single species in California, where they are frequent to common members of chaparral (*Pickeringia*) or woodland communities (*Thermopsis*) across the NCBDA. In contrast, the very similar genus *Lupinus* contains a total of 60–70 species in California, dominated by perennials, a number of which are in the NCBDA. *Pickeringia* and *Thermopsis* are somewhat isolated within the Fabaceae, based on the state of their stamen filaments, that are free and separate, whereas in nearly all other California genera of the family, including *Lupinus*, nine of the ten filaments are fused. These three genera resemble each other in most other characters and often grow in similar habitats. Can it be that the mere difference between free vs. fused stamen filaments can be the cause of this great difference in speciation? The development, floral biology and pollination biology of these three genera is well worth investigating.

The present review has shown that recognition of the North Coast Biodiversity Arena has not solved any problems associated with diversity of speciation or with phylogeny. Nevertheless it has been the source of research guidelines and of groups of species highly suitable for this purpose. These guidelines can be applied equally well to the more challenging problems posed by tropical floras. To those young men and women who have become "hooked" on the idea of using observations on natural history to solve problems of plant evolution, we can give you a relevant quotation, but we can't give you its source. The senior author learned it 80 years ago, when playing with Richter's Anchor Blocks:

"We play at paste 'til qualified for pearl
then throw the paste aside and think ourselves deceived
the shapes, though, are similar and our rough hands carve
diamonds while playing with sand."

ACKNOWLEDGMENTS

We are very grateful to the numerous reserve managers, private landowners, and botanists who so graciously allowed access to the properties for which they are responsible, or of which they have special knowledge. In particular, we would like to thank Joe Callizo of Pope Valley for his extensive assistance, Harry Tranmer and Pete Imboden at Mt. George, David Auerbach at Archer Taylor Reserve, Dr. Gilbert Muth of Pacific Union College, Alita Apgar at Cavedale Road for her willing assistance and interest, the Roth family at Aetna Springs, Ann Howald of the California Dept. of Fish & Game, Dr. Charles Quibell of Sonoma State University, and Walter and Irja Knight for sharing their incredible knowledge of Napa and Sonoma counties. Without the generous assistance of these folks our field visits would have been much more difficult and infinitely less enjoyable. To the reviewers of this manuscript in its 'roughest' form, for their patience we are deeply appreciative.

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(Received 31 Aug 1994; accepted 20 Jan 1995)

APPENDIX I. ESTABLISHED PUBLIC AND PRIVATE RESERVES, PARKS AND FORESTS WITHIN THE NORTH COAST BIODIVERSITY AREA. This compendium is not exhaustive; it is intended to emphasize the large number of potential sites available to those planning research or educational excursions within the NCBDA. Those interested in visiting any of these sites to ascertain their suitability for projects or class visits should contact the organization or agency listed. There are in addition large tracts of land within the NCBDA administered by the United States Forest Service. National Forest land is most extensive in the area north of Clear Lake. Sites are grouped alphabetically within sector and the major points of botanical interest at each site are listed. Abbreviations: *Land administrators:* California Department of Parks and Recreation (CDPR), Napa Land Trust, Napa California (NLT), California Department of Fish & Game (CDFG), California Department of Forestry (CDF), California Academy of Sciences (CAS), United States Forest Service (USFS), The Nature Conservancy (TNC), University of California Natural Reserve System (UC). *Botanical or Geologic Specialty:* *Botanical Specialty:* Coast interface (CI), mixed evergreen (ME), mixed evergreen with *Sequoia* (ME-*Sequoia*), riparian (R), riparian with *Sequoia* dominant (R-*Sequoia*), chaparral (C), single tree-species forest/bishop pine (STF/Bishop Pine), single tree-species forest/*Cupressus* (STF/*Cupressus*), single tree-species forest/*Quercus wislizenii* (STF/*Quercus*), oak woodlands-various species mixtures (OW), oak woodlands/savanna (OW/S). *Geologic Specialty:* Serpentine (SERP), hard rock volcanics (VOL), fossilized volcanic ash (ASH).

Site name	Administrator	Bot/Geo specialty
Western sector		
Armstrong Redwoods State Reserve	CDPR	<i>Sequoia</i> , R
Austin Creek State Recreation Area	CDPR	SERP, ME- <i>Sequoia</i> , C, R, OW
Fort Ross State Historical Park	CDPR	STF/Bishop Pine

APPENDIX I. CONTINUED

Site name	Administrator	Bot/Geo specialty
Harrison Grade Ecological Reserve	CDFG	SERP, STF/ <i>Cupressus</i>
Kruse Rhododendron State Reserve	CDPR	ME- <i>Sequoia</i>
Laguna de Santa Rosa Ecological Reserve	CDFG	R
Salt Point State Park	CDPR	STF/BP, CI
Sonoma State Beaches	CDPR	CI
Stillwater Cove County Park	County of Sonoma	CI
Yorkville Ecological Reserve	CDFG	SERP
		Central Sector
Annadel State Park	CDPR	ME- <i>Sequoia</i>
Archer Taylor Reserve	NLT	ME- <i>Sequoia</i> , C, ASH
Bothe-NAPA Valley State Park	CDPR	ME- <i>Sequoia</i>
Bouverie Reserve	NLT	ME, VOL
Fairfield Osborne Reserve	TNC	wetland, vernal pool, R, OW, ME
Hood Mountain Regional Park	County of Sonoma	ME
Lake Hennessey Rec. Area	City of Napa	OW, SERP
Las Posadas State Forest	CDF	ME, R- <i>Sequoia</i>
Mount George Reserve	NLT	C, VOL
NAPA River Eco. Reserve	CDFG	R
NAPA River State Park	CDPR	R
Pepperwood Reserve	CAS	OW, ME, SERP
Robert Louis Stevenson State Park	CDPR	ME, C
Sonoma Valley Regional Park	County of Sonoma	OW, ME
Sugarloaf Ridge State Park	CDPR	ME, R- <i>Sequoia</i> , C, OW/S, SERP, VOL
		Eastern Sector
Frenzel Creek Research Natural Area	USFS	STF/ <i>Cupressus</i> , R, SERP
Lake Berryessa State Recreation Area	CDPR	OW, C, STF/ <i>Cupressus</i> , SERP
Quail Ridge Reserve	UC	OW, C
Stebbins Cold Canyon Reserve	UC	STF/ <i>Quercus</i> , OW/S, C, R
Wantraub Reserve, Pope Valley	NLT	OW/S

APPENDIX II. PUBLIC AND PRIVATE FOUR YEAR UNIVERSITIES WITHIN A CONVENIENT DISTANCE OF THE NORTH COAST BIODIVERSITY AREA.

University or college	Location	County
California State University	Chico	Butte
California State University	Hayward	Alameda
California State University	Humboldt	Humboldt
California State University	Sacramento	Sacramento
California State University	Sonoma	Sonoma
California State University	Stanislaus	Stanislaus
Mills College	Oakland	Alameda
Pacific Union College	Angwin	Napa
San Francisco State University		San Francisco
San Jose State University		Santa Clara
Stanford University	Stanford	San Mateo
University of California	Berkeley	Alameda
University of California	Davis	Yolo
University of California	Santa Cruz	Santa Cruz
University of the Pacific	Stockton	San Joaquin

THE UNIVERSITY, THE STATE, AND THE LOSS OF PLANT DIVERSITY

PETER H. RAVEN

Missouri Botanical Garden, St. Louis, MO 63166

My roots in Berkeley are deep, a fact that adds to a profound sense of satisfaction on this auspicious occasion. My grandfather was in the first class to graduate from Bolt Hall; his grandfather, Patrick Breen, who came to California in 1846 in the Donner Party, left a diary that is one of the treasures of the Bancroft Library; and my mother graduated from this beautiful campus in the year when the Life Science Building first came into use. For these and many other reasons, I take great personal satisfaction in the presentation of these outstanding new facilities here this evening. It was an extraordinarily satisfying experience for me to enter Berkeley myself as an undergraduate student in 1955, a much-appreciated start to my own career. For these personal reasons, it is a special satisfaction for me to see what an outstanding contribution the University has made to systematic biology by refurbishing these facilities so beautifully: they will serve generations of Californians and others well, and help this proud institution to remain in the forefront of those which recognize the importance of biodiversity as an integral part of the science of biology, as well as for human progress in the future.

There are very few universities that possess the ample resources of specimens, of library materials, of archives, and of people that are present on this campus. In consequence of these assets, the potential for future service is truly impressive. As time goes by, much of the focus will doubtless continue to be on the plants of California, which have interested and delighted all those who have come into contact with them or lived among the hills and valleys of this fascinating, diverse, and truly wonderful State. But the plants and the natural communities of which they are a part have changed drastically just since I was a boy, and they are continuing to change at an alarming rate. What are the dimensions of this problem, and how shall we deal with it?

The fields of wildflowers near the places where we grew up have, in many cases, vanished; the meadowlarks have moved further back into the hills; and California is not the place that it was a few decades ago. I don't feel that I have attained any very great age, and yet I can easily remember driving down to Hollister and San Juan Bautista from San Francisco on basically a two-lane or three-lane road through

orchards, with no freeways anywhere. Such memories of the Bay Area in the 1930's and 1940's illustrate vividly how the region has changed, and in turn instruct us in the importance of caring properly for this State, with all of its biological riches. The University Herbarium, and particularly, the Jepson Herbarium, have central roles to play in this effort, through their studies, through the students who benefit from them, and through the many publics that they serve.

Among the various ways in which people have viewed the natural scene in California, I have always enjoyed Herb Caen's expression: "A true Californian is someone who knows that the hills are naturally a golden brown, which is interrupted briefly in winter by the appearance of a greenish scum, which soon disappears, returning them to their natural glory." I have found delight of a different kind in John Muir's view, when he wrote, remembering a scene that he viewed in April 1868: "Looking eastward from the summit of Pacheco Pass, one shining morning, I found before me a landscape that, after all my wandering, still appears as the most beautiful I have ever beheld. At my feet lay the great central valley of California, level and flowery, like a lake of pure sunshine, forty or fifty miles wide, five hundred miles long, one rich furred garden of yellow Compositae. And from the eastern boundary of this golden flower bed rose the mighty Sierra, miles in height, and so gloriously colored and radiant, it seemed not clothed with light, but wholly composed of it, like the wall of some celestial city. Along the top, and extending a good way down, was a rich pearly gray belt of snow, below it, a belt of blue and dark purple, marking the extension of the forests and stretching along the base of the range, a broad belt of rose purple. All these colors, from the blue sky to the yellow valley, smoothly blending as they do in a rainbow, making a wall of light ineffably fine."

Personally, I became fascinated with the plants of California when I was eight or nine years old. Rather than gaining an interest in natural history, I simply retained my childhood interest, an interest that many lose as they grow older. I can remember as vividly as if it were yesterday crossing over to Marin County and seeing *Sanicula arctopoides* blooming in the spring woods—what a unique and interesting plant! I can also remember visiting Bernal Heights in San Francisco for the first time in spring, searching for what Jepson called *Dodecatheon hendersonii* var. *bernalianum*, and the joy of finding those beautiful flowers in abundance. And then I can remember being in the redwood forests in the Santa Cruz Mountains and seeing *Clintonia andrewsiana*, with its extraordinary blue fruits, for the first time. These were among the plants that impressed me deeply when I was a boy.

Another of the reasons that I am so glad to be here, is the memory of the enormous effect that Jepson's *Manual* had on me: how helpful

it was in my studies of California plants. Here in a single volume one could look up the characteristics and geographical ranges of all the plants of California! Jepson was a master at describing plants. He would use very few words, and they were exactly the words that were most helpful in understanding what a particular plant looked like. Such skills were, of course, based on his lifetime of experience with those plants, and the way that he cherished them, which Lincoln Constance brought out so beautifully for us in his lecture last evening. When I was eight years old, I first visited the student section of the California Academy of Sciences, and was allowed to join in the autumn of 1944. Subsequently, I was invited to meet Alice Eastwood, then 90 years old, to ask her opinion about the identities of some plants that I had collected. So I took my plants, which I had mounted on sheets of herbarium paper, and confronted Miss Eastwood, who was sitting, smiling, in her office. If I seemed to have been a shy undergraduate at Berkeley, you should have seen me at nine years old confronting Alice Eastwood—but I shall always remember how kind she was to me. Among my plants was a specimen of *Rosa gymnocarpa* with a single fruit. On seeing it, Miss Eastwood exclaimed, "Oh, it's so good that you collected the fruit, because you can see that the sepals have dropped off, and because the specimen is so complete, I can tell you that it is *Rosa gymnocarpa*." That was certainly a kind and encouraging comment, especially when one remembers that I was a tenth of her age at the time!

With your permission, I would like to dedicate these remarks to the memory of John Thomas Howell, one of those who was encouraged in his pursuit of botany by Jepson. John Thomas Howell was born in Merced, November 6, 1903, and passed away on May 7, 1994 in San Rafael. His 70 years of study of plants, chiefly those of California and the West, and his 54,000 collections, established a permanent record of the plants of California and some of the West during the middle decades of the 20th century.

Tom was encouraged by his parents and particularly by his Merced High School chemistry teacher. Entering Berkeley, he soon fell under the influence of Jepson and decided to major in botany. I believe that it may have been a natural result of the encouragement that he received himself in his early years that he so consistently encouraged others, not only in botany, but generally. Although he was ever anxious to complete his own work, he still was ready to take the time to provide advice and counsel, and to talk about the intricate details of variation that the plants of California exhibit. He shared his delight in those plants—in their beauty, in their variety, and in the wonderful places where they grow—with many people throughout his life.

I became acquainted with Mr. Howell in 1945 or 1946, and there followed a whole series of wonderful opportunities and experiences

for me. For example, I was delighted when I found what was then called *Pentachaeta bellidiflora* at a new locality in Marin County just in time to get my collection incorporated into the first edition of *Marin Flora*. It was at Tom's suggestion that I joined the Sierra Club, becoming about the 18,500th member in 1948, at the age of 12; Tom had been active in the Club since the early 1940's. I visited the Sierra Club lodge at Norden in 1949, and again in 1950, and that's when my plant collecting began to get serious, and I began to consult the Academy herbarium. I well remember going there and trying to figure out what *Stipa lemmonii* was, and how it could be distinguished from related species, having no idea that much later it would be blessed with the name *Achnatherum*! At about the same time, I began writing articles, initially for *Leaflets of Western Botany*, a journal that was established by Alice Eastwood and Tom Howell in 1931, and was published until 1968. The journal was filled with Howelliana such as "A botanist gambles in Reno" and "Two confused western daisies," containing a rich store of knowledge about plants, and especially about the plants of California. In that same period of my life, and still with some discomfort after all of the intervening years, I can remember Tom telling me, after I had written my first few short articles, that I had mastered the necessary jargon, and could go on writing articles forever, whether I had anything to say or not!

In those years also I had the wonderful pleasure of joining the 1950 Sierra Club Base Camp trip, where I first met Ledyard Stebbins and his daughter Edie, thus initiating a lifelong friendship with that remarkable man, who has contributed so much to the study and understanding of California plants and of plants generally. You can imagine what a treat it was for me, at the age of fourteen, to be sharing a tent with Ledyard, who was then still at Berkeley, about to publish his monumental *Variation and Evolution in Plants*, just on the verge of moving permanently to Davis. Through him that summer I began to glimpse the power of evolutionary studies, and the joy associated with the understanding that such a perspective brought. My subsequent years at Berkeley, and in graduate school at UCLA, where I studied with Harlan Lewis, were very happy ones, and so it has been all of my professional life, for which I am truly grateful.

Allow me to share with you a few more thoughts about Tom Howell. At a time when getting everything done as rapidly as possible, publishing as much as widely as possible, and working toward the improvement of our material status threaten to become universal goals, I recall, for some curious reason, Tom's lifelong delight in the way that the specimen of *Iris hartwegii* that he pressed when he went to Wawona as a counselor at the end of his first year at Berkeley, retained the color of its flowers. It was a beautiful specimen, and he

took great satisfaction in that simple fact. I think that his appreciation of his modest accomplishment might, in some way, be taken to represent for us the kind of depth and fullness of experience that is possible, and that certainly help to make botany, and perhaps even life, really worthwhile.

Tom Howell had a great sense of fun. He loved plants and people. He was thoughtful and generous with his time. He really was a fine role model, and I'm glad to have known him so well during my teen years. One thing that he forced me to do was to prepare handwritten herbarium labels, which were the only kind that he considered authentic. After I wrote a few, and he saw that they were illegible, he insisted that I improve my handwriting—not a bad idea at all. During my teenage years, I volunteered in the Academy's botany department, for example breaking down Henry Pollard's often massive herbarium specimens from the Ojai Valley so that they could be mounted. Years later, I remarked to Mr. Howell that I used to greatly enjoy coming in after school and volunteering, whereupon he reminded me of the "bait," a Hershey bar that he placed each day in the drawer of my desk!

Let us turn now to the plants of California. Exactly two centuries ago, in 1794, Captain George Vancouver was sailing away from the coast of California, the third European expedition to bring back some knowledge of our plants. Among other regions, he visited the Monterey area, and near Santa Cruz, Archibald Menzies, a scientific passenger on the voyage, discovered redwoods—the plants of the west coast began to be understood for the first time. A hundred years later, in 1894, Edward Lee Greene, after nine successful years at Berkeley, was contemplating moving to the Catholic University. During his residence at Berkeley, Greene contributed fundamentally to the establishment of a tradition of resident botanists studying the plants of the State, and laid the foundation for botany on this campus. In that same year, Greene's students, Ivar Tidestrom and Willis Linn Jepson, were helping him to plant the first specimens in the young botanical garden that they were building along Strawberry Creek. And I couldn't help thinking, as I was walking down through the campus this afternoon, that they must have enjoyed seeing some of the same California laurel trees and hearing the calls of the ancestors of the same blue jays that we hear there today. Such thoughts provide a peaceful sense of continuity, as well as a vision of a long and prosperous future, for this institution.

There are some 18,000 species of vascular plants in the United States and Canada, about a third of them occurring within the borders of California. About 5000 of those are native, about a quarter of them endemic to the State. For the California Floristic Province, west of the mountains and the deserts, but including southwestern Oregon and northwestern Baja California, there are about 4000 na-

tive species, about half of them endemic, including about 50 endemic genera. By world standards, those are impressive totals; and the intricate patterns of variation of our plants, related to the intricacies of our geography, are as complex and interesting as those found anywhere.

The University, its herbarium, and the Jepson Herbarium in particular, with its specimens, library, and professional staff, is in a unique position to contribute to the interpretation and increase of information about those plants in the future, as it has done in the past. The herbarium includes about 1.7 million species, with about as many at the California Academy of Sciences, including the Dudley Herbarium—probably nearly four million specimens in the Bay Area as a whole, and thus one of the world's largest collections of plants. The Berkeley campus likewise is home to one of the world's premier botanical gardens, in terms of native-collected and documented material. The development of the garden over the past 30 years has been extraordinary, and is a real tribute to the efforts of Bob Ornduff and others who have served as directors during that period of time, as well as the talented staff members who have helped to assemble this remarkable resource. Those members of the general public who have supported the garden through thick and thin are likewise to be congratulated for what they have helped to achieve.

The potential for service for Berkeley in the future is based squarely on the fact that its herbarium, library, and garden are parts of a great university, with all of its wonderful and diverse educational possibilities, with scholars representing many disciplines, with other libraries, with world-class computer facilities, and all of the assets that an institution of this quality and scope confers. This complexity and richness allows students and the public to celebrate and learn about plants in all of their diversity and in all of the ways in which they relate to humans. A great urban center, located in a region that is home to one of the most fascinating floras in the world, and in a State that is known for global leadership—these are certainly the ingredients of greatness.

Now let us consider the discipline of systematics. Systematics is a composite discipline that requires a number of different skills and operates through several more-or-less distinct stages. First, as Barbara Ertter has often stressed well, the primary factor that underlies systematics and makes it possible is the ability to find and to understand organisms as they exist in nature. Excited by the many new and rapidly growing fields of investigation associated with modern biology, we sometimes forget that it is the actual plants, their ranges and other features, and their status that we need to investigate first. Without the continuous acquisition of such knowledge, so fundamental for everything else; without the ability to recognize and distinguish the kinds of organisms; without the careful documentation

of what we learn in biological collections, nothing else in systematic or evolutionary biology is possible. For example, E.O. Wilson has often pointed out termites and ants together comprise about a third of the animal bio-mass in the world, but there are only about twenty scientists who actually have the ability to identify and to classify them systematically. The picture for fungi is even worse, despite the economic and ecological importance of these organisms, and the fact that we have so far named fewer than 70,000 of an estimated 1.5 million species. Difficulties in interpreting the taxa of endangered and threatened groups of plants in California, such as those of the *Chorizanthe valida* group, illustrate a similar point: regardless of our laws, we cannot act on them without understanding the limits of the taxa involved. Only a scientist who is knowledgeable about a particular group of organisms can sort them out properly, understand them, and interpret their patterns of variation. Without such knowledge and the associated studies and documentation, nothing else in biology can be accomplished in a comparative, evolutionary context: cladistics, macromolecular studies, biogeography, every elegant approach to the diversity of life on Earth is impossible, irreproducible, and trivial. Can most macromolecular comparisons between organisms be replicated? Only if there are vouchers—in a world where less than 15% of the total kinds of organisms have even been named, it is not good enough to assume that all are known, and that any sample will do.

In terms of learning about the plants of California properly, we can reasonably take delight in the activities of state agencies, The Nature Conservancy, private consultants, the California Native Plant Society, and similar organizations, but we still need the Jepsons, the Eastwoods, the Howells, the Ferrises, the Constances, the Ornduffs, the Mishlers, and some of these individuals will best be located in universities, where they are able to educate students and to provide, if you will, a kind of a scholarly bridge, a foundation, for all of the people and agencies that are concerned with the plants of the State. Without that essential ingredient—without a serious study of these organisms and how to recognize them, to interact with them, and to train students in the universities and in the academic places—we won't have the kind of comprehensive system that we really need in order to deal with the plants of California.

And it is diversity that makes biology interesting and worthwhile. Our knowledge of diversity, our ability to deal with it, and to understand what and where it is, is the basis of all of a great many of our human activities, whether we are dealing with aesthetics, art, poetry, management, restoration ecology, controlling weeds, growing lush lawns or fascinating displays of native plants, practicing better agriculture, undertaking genetic engineering, or conserving the organisms that nurture and sustain our lives. Without that funda-

mental devotion to learning about organisms, nothing else is meaningful.

The second major area of botanical studies that I would like to emphasize concerns the synthesis of information—the production of classifications. Although we are all deeply and properly impressed with the power of cladistic methods of analysis, and with the exciting new information that is becoming available as a result of macro-molecular comparisons, as well as with the importance of information retrieval, it is ultimately the scientific process of classification—of grouping organisms into meaningful units—that makes possible everything else in systematic, evolutionary, and environmental biology, and which ultimately gives meaning to all of biology. A community-based project such as the *Flora of North America*, a program that involves about 30 collaborating institutions throughout the United States and Canada; hundreds of individuals; and a very careful and rigorous editorial process, basically depends on a rigorous scientific process in the course of which the kinds of plants that occur in the region are recognized and delineated. It is misleading, virtually tragic, to assume that everything is known about these plants, and that the units can be recognized as easily as looking up widgets in a Sears Catalogue, or a Peterson guide to the birds of a given area. To inventory, to understand, the plants of the region, science and agreement are necessary first; once that synthetic and community-wide process has been completed, then and only then it becomes possible to computerize the data, pop label information into a computer, get it back out, and stockpile the additional data that are accumulated for future use. When we become so fascinated with the rather simple technology of information retrieval that we forget what surveying and inventorying organisms is all about, then we forget our science and lose the opportunity to understand organisms properly. It is very useful to write legible labels, to store specimens in a logical system, and to be able to retrieve the information that is recorded on their labels—but it isn't science.

Science is synthesis, and agreement, and investigation, and badly needs our continued attention, and our support. *Flora of North America* is not a specimen-based atlas of the plants of North America, but rather an international, community-based program that will ultimately provide a sound, scientific basis of classification for the plants of the region that is necessary for such a technical exercise to be meaningful. To appreciate my point, consult the treatments of *Botrychium* or *Eriogonum* in the flora, and consider what computerizing the labels of those groups would have meant without the synthetic, continental account represented by the book!

Moving to another important area of activity in systematic biology, consider biosystematics. California is the place where much

of this synthetic area has developed, a relationship that is perhaps not surprising considering the remarkable flora of the State and the outstanding institutions located in it. Some of the deepest roots of biosystematics extend from the experiments of which Harvey Monroe Hall, then at Berkeley, was really the guiding light; he put together the team that made it happen. Although biosystematics has flourished in California, and a great deal of information is available about some groups of plants here, a great deal remains to be done.

For the overall advance of understanding plant evolution in the region, and generally, it would be desirable to select plants with characteristics that differ from those of the groups that have been studied more or less comprehensively already. Now here's an area where collaboration between botanical gardens and herbaria systematic botanists is really important. For example, we know a lot about the biosystematics of tarweeds, *Potentilla glandulosa*, and of *Lasthenia*, but we know next to nothing about the analogous features of *Arctostaphylos*, *Garrya*, or *Fremontodendron*. In principle, the appropriate studies could be carried out in botanical gardens, where the experimental hybrids could be made and examined years later when they reached reproductive maturity. Although investigations of this sort are not suitable for doctoral dissertations, people who have long-term employment and access to the necessary field space might appropriately plan such experiments and carry them out. Doing so would enhance our knowledge of patterns of variation and evolution of some very different groups of California plants greatly, and assist in the development of a synthetic theory of plant evolution. What sorts of reproductive barriers exist in these groups of woody plants, how has past hybridization affected them, how do they vary in cultivation—these are all questions that should be addressed in a comprehensive way.

Now let's consider the area of phylogenetic analysis. We now have access to many wonderful experimental and analytical techniques, techniques that will allow us to determine clearly, and at long last, whether *Simmondsia* belongs to the Buxaceae or not, or in the Euphorbiaceae, or if it doesn't, what are its relatives? For that matter, is Euphorbiaceae a homogeneous family, or a collection of divergent groups linked by a superficial similarity? As a result of our ability to provide secure answers to such questions, we are clearly living in the most exciting period ever for the study of plant phylogeny, a period in which we shall understand well for the first time the phylogenetic structures of individual families, the relationships of families, and the evolutionary history of phyla and kingdoms of organisms. Within no more than a decade, we shall have achieved a relatively complete solution to problems that have preoccupied botanists for centuries, and a vision of plant evolution that will exceed

anything we can imagine now. With such a framework, the analysis of other features of plants, such as reproductive biology, embryology, and the nature of secondary metabolites, will be enhanced greatly, becoming increasingly productive and interesting.

Finally, I would like to mention the area of information retrieval, treated narrowly as a virtual synonym of electronic data processing by most people today. Given the millions of poorly-understood species of organisms that exist, with essentially unlimited observations possible about each of them, it is obvious that such methods must be applied as a matter of simple common sense. Indeed, it is increasingly difficult to imagine significant progress in the field without them: the actual and potential data are simply too extensive. Consider the hundreds of millions of herbarium specimens, or the estimated 25 million mounted prepared specimens of insects in The Natural History Museum, London—resources that obviously can be utilized on a wide scale only by organizing and thus making available the information that they represent. Noteworthy in this area is the Museum Informatics Program here at Berkeley, which has been an important contributor to advances in this field for a number of years.

An important aspect of the formation of electronic data bases is that it no longer matters much in principle how individual herbaria are organized, or whether they are physically combined or not—except in terms of efficiency of storage arrangements. The evident growing collaboration between the University Herbarium at Berkeley, the California Academy of Sciences and Dudley Herbarium, and other similar institutions in the State is an important element in the management of plant resources in California, including their conservation, and one that richly deserves direct State support. The growing numbers of vouchers that are being produced as a result of the operation of State and Federal programs need to be accumulated efficiently, and to be entered into the State data base in such a way that their existence will expedite further research and more effective management plans. In general, the linkages between universities, museums, botanical gardens, the Heritage Program established by The Nature Conservancy, other conservation groups, and all parties interested in the sustainability of California need to be strengthened for the common good. A comprehensive plan for the conservation of California's plants, both in nature and botanical gardens and similar facilities, ought to be organized promptly to serve the mandates of the State and Federal governments in this area effectively. Such a plan should be based on the data that will eventually be gathered into the SMASCH database, which in principle will eventually include the available information about the plants of the State, and provide a means for determining their status on an ongoing basis. Linkages with other nationally significant databases, such as the 600,000 specimens in the database we maintain at the Missouri

Botanical Garden, ought to be forged so that the resulting system can serve global as well as local needs. Access to databases such as that of the Paleontology Museum here, or the Missouri Botanical Garden's database through the World-Wide-Web or gopher systems is becoming standard, both of these databases being consulted by tens of thousands of users monthly.

I know that we share a profound joy in the privilege of studying and learning about one of the most remarkable and beautiful assemblages of plants anywhere on Earth. Moreover, the vision of a network of Californians—amateur, non-academic, professional—all working together around this common theme, is truly impressive. Special praise is due to the California Native Plant Society, with well over 10,000 members throughout the State, and specifically for the role of Ledyard Stebbins in inspiring the group during its formative period. Throughout his long and distinguished career, Ledyard has not only contributed fundamentally to our understanding of plant evolution, he has inspired people everywhere with his love of plants and called their attention to the need to appreciate and conserve them. Every resident of California has a right to feel the special joy that we are celebrating here this evening, a joy based on an appreciation of the plants of the State and the intricacies of their biology, a subject of which we never tire. A few dozen species have already been lost in California: let's be certain that there are no more.

Perhaps a network of botanical gardens, or two networks, one in Northern California and one in Southern California, could be organized to address this task. The Center for Plant Conservation, of which there are currently two members, the garden here in Berkeley and Rancho Santa Ana, in California, has implemented a network of this sort in Hawaii, and the ingredients are certainly here for an all-out effort to preserve native plants. Who will take the lead in mounting such an effort?

To conclude with a few major themes, I shall begin with education. The University has an important role to play not only with regard to its students, but for its many publics as well. With a firm focus on organisms, their characteristics and geographical ranges, the University program will always have a great deal to offer in this area, and many willing learners. The kind of commitment that the University has made in this magnificently refurbished Valley Life Science Building marks its commitment to organismal biology, and to continued leadership in this field.

To speak of the role of the State, California remains an extraordinary world leader, despite its recent economic problems. Within California, the Bay Area is a particular center for innovation, and this institution perhaps the strongest public university in the world. In this context, the kind of foresight that Robert Gordon Sproul

exhibited in building the university during the Great Depression provides inspiration—the kind of inspiration that we sorely need in confronting an uncertain future. Similar foresight, and similar leadership, is badly needed in the world today, with patterns of consumption and uses of technology that cannot be sustained. With vision, resources can always be found; without it, nothing can be accomplished. The organization of the California Desert Bill, which will leave such a significant heritage for future generations, provides a clear example of what such leadership can be. The challenge of using the unimaginable resources of this university community and this State to provide a worthy model for the solution of global problems transcends current economic woes, and provides a challenge of transcendent importance for local leaders at all levels.

In conclusion, it is worth mentioning once more the remarkable contributions of Willis Linn Jepson. Through a lifetime of perceptive studies, he gave us the first clear understanding of the flora of California. The joy that he felt in his boyhood in the Sacramento Valley, and in exploring the Vaca Mountains and further afield, we feel in coming together on this singular occasion, in the pleasure of being citizens of the most prosperous and blessed nation on Earth, of enjoying the beautiful plants that we have been discussing and the landscapes that they fill with greens, greys, and browns, and in the intellectual tools that we have gained, and which will help us to know more and more about these plants and the principles of our survival. Our privileged position brings with it opportunities, challenges, and obligations, ones that we shall be dealing with as well as we can for as long as we are able.

(Received 26 July 1994; accepted 28 Oct 1994)

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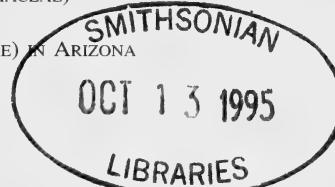
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MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$50 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to the treasurer.

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GENETIC DIVERSITY IN POPULATIONS OF KINCAID'S LUPINE, HOST PLANT OF FENDER'S BLUE BUTTERFLY

AARON LISTON, KIMBERLY ST. HILAIRE, and MARK V. WILSON

Department of Botany and Plant Pathology,
Oregon State University,
Corvallis, OR 97331-2902, USA

ABSTRACT

Kincaid's lupine (*Lupinus sulphureus* ssp. *kincaidii*) is the primary host plant of the endangered Fender's blue butterfly (*Icaricia icarioides fenderi*). Both species are found in remnant upland prairies in the Willamette Valley of western Oregon, a habitat that is threatened by agriculture and urbanization. Enzyme electrophoresis was used to characterize the levels and distribution of genetic diversity in Kincaid's lupine. Eight populations of Kincaid's lupine exhibited high genetic identities (mean interpopulational $I = 0.984$) and low levels of genetic differentiation among populations ($G_{ST} = 0.119$). Although gene flow between the disjunct populations is limited at present, the species may have had a more continuous distribution prior to the agriculturalization of the past 150 years. At the Baskett Butte site, all plants considered to represent Kincaid's lupine had alleles that were otherwise restricted to spur lupine (*L. arbustus*). In addition, two clones composed of genetically identical individuals with fixed heterozygosity at four loci were identified at Baskett Butte. We suggest that hybridization between the two species is responsible for these findings.

Grasslands dominated by native bunch grasses extended over at least one million acres in the Willamette Valley prior to the introduction of agriculture, livestock grazing and urban development in the nineteenth century (Franklin and Dyrness 1973). Today, fewer than 1000 acres of high quality native grasslands are known to remain in the Willamette Valley. These upland prairies support a variety of native grasses and perennial forbs. An animal species of particular conservation interest, the endemic Fender's blue butterfly (*Icaricia icarioides fenderi*), is known from only twelve upland prairie sites within Oregon's Willamette Valley (Hammond and Wilson 1993).

The primary larval host plant of this lycaenid butterfly is Kincaid's lupine (*Lupinus sulphureus* Hooker ssp. *kincaidii* (Smith) Phillips). This member of the legume family is known from approximately 40 sites in the Willamette Valley of Oregon, south to Douglas County, and from a single location in southern Washington's Puget Trough (Kuykendall and Kaye 1993). Kincaid's lupine is present at all twelve known Fender's blue populations. However, at three of the sites, spur lupine (*L. arbustus* Douglas ex Lindley) or sickle-keeled lupine (*L. albicaulis* Hooker) also support Fender's blue (Hammond and

Wilson 1993). The nomenclature of *L. arbustus* follows Barneby (1989); the name *L. laxiflorus* Douglas ex Lindley has been misapplied to this species in the past.

Kincaid's lupine is a potentially long-lived perennial herb (at least 25 years old in one excavated individual, M. Wilson unpublished data) that can spread vegetatively. Populations are disjunct and generally small (< 10 individuals), although a few populations may have more than 1000 individuals. The fragmented distribution of the species in the Willamette Valley is apparently due to the conversion of suitable habitat to agricultural and urban uses. Kincaid's lupine is self-incompatible, and is pollinated by native bees and flies (T. Kaye unpublished data; P. Hammond personal communication). Measured seed production rates are low: 1.8 seeds/fruit in 1990 (T. Kaye unpublished data) and 0.3–1.2 seeds/fruit in 1992 (Kuykendall and Kaye 1993). A chromosome count of $n=24$ has been reported for a Willamette Valley population of Kincaid's lupine (Phillips 1957). This chromosome number is the most common in North America *Lupinus* (Goldblatt 1981). Although this number is considered "tetraploid" (Phillips 1957), isozyme studies in *Lupinus* suggest that most loci do not show duplicate expression (Wolko and Weeden 1989).

Fender's blue butterfly and Kincaid's lupine are both considered "threatened throughout [their] range" (Oregon Natural Heritage Program 1993). The survival of Fender's blue butterfly will require the careful management and perhaps restoration of its unique habitat. Efforts to preserve Fender's blue will benefit from a full understanding of the biology of the primary host plant. In this study we use the technique of enzyme electrophoresis to estimate the levels and distribution of genetic variation in Kincaid's lupine. This technique is now widely used to infer the genetic structure of plant species of conservation concern (Karron 1987; Waller et al. 1987; Lesica et al. 1988; Pleasants and Wendel 1989; Prober et al. 1990; Les et al. 1991; Soltis et al. 1992; Godt and Hamrick 1993). The present study is unique in that the genetic characterization of a rare plant species is also of relevance to the conservation of the endangered Fender's blue butterfly.

Enzyme electrophoresis is used in this study to determine 1) if genetic differentiation exists among populations; 2) which populations contain the most genetic variation; 3) the patterns of genetic partitioning within populations; and 4) whether hybridization takes place when Kincaid's lupine is sympatric with other lupines.

METHODS

Populations of Kincaid's lupine were sampled at eight sites in the Willamette Valley of Oregon and the single known location in south-

TABLE 1. ALLOZYME VARIATION AND MEASURES OF GENETIC DIVERSITY AT THE POPULATION LEVEL IN KINCAID'S LUPINE. N = average number of individuals scored per locus. P = percentage polymorphic loci at the 0.99 level. A_p = average number of alleles at polymorphic loci. H_o = observed heterozygosity. H_u = expected heterozygosity, unbiased for sample size, under Hardy-Weinberg equilibrium. F = fixation index, calculated from observed and expected heterozygosity for polymorphic loci. No significant deviations from Hardy-Weinberg expectations were observed.

Abbreviation	Population Subpopulation	Location	Fender's Blue	N	P (%)	A_p	H_o	H_u	F
BC	Boisfort Cemetery	Lewis Co., WA	absent	22.3	13.3	2.50	0.081	0.070	-0.156
	Oak Ridge	Yamhill Co., OR	present	18.7	33.3	2.40	0.150	0.135	-0.048
OR	Mill Creek	Polk Co., OR	absent	16.9	26.7	2.50	0.130	0.107	-0.301
MC	McTimmonds Valley	Polk Co., OR	present	14.0	26.7	2.25	0.100	0.096	-0.153
MV	McDonald Forest	Benton Co., OR	present	38.3	33.3	2.20	0.090	0.096	-0.037
MF	Upper			19.6	20.0	2.33	0.078	0.082	-0.107
MF-1				18.7	33.3	2.20	0.103	0.105	-0.065
MF-2	Lower			18.7	26.7	2.25	0.111	0.111	0.063
WH		Benton Co., OR	present	21.2	40.0	2.33	0.135	0.126	-0.136
WH	West Hills Road	Lane Co., OR	absent	22.2	33.3	2.20	0.153	0.146	-0.152
HR	Hillaire Road	Lane Co., OR	present						
WC	Willow Creek	Polk Co., OR	present						
BB	Baskett Butte						see Table 2		
Mean				21.5	29.2	2.33	0.134	0.111	-0.115

ern Washington (Table 1). Fender's blue butterfly is present at six of these sites, representing half of its known occurrences. The other three sites do not support Fender's blue. The McDonald Forest site of Kincaid's lupine was represented by an upper and lower subpopulation separated by 100 meters. The site at Baskett Butte (within the Baskett Slough National Wildlife Refuge) was sampled as five subpopulations (Table 2). These represented *L. arbustus* (BB-arb-1, BB-arb-2), *L. s. kincaidii* (BB-kin-1, BB-kin-2), and a small group of morphologically intermediate plants considered putative hybrids (BB-int). The north meadow subpopulation (BB-arb-2) is located ca. 500 meters from the remaining four subpopulations, which are located on the summit and southwest slope of Baskett Butte proper.

Population samples were made in the spring of 1991 and 1992. A total of 18–24 individuals were sampled per population (Table 1). A single leaf was collected from plants separated by at least one meter. Leaves were transported to the laboratory on ice, and frozen at –80°C until analysis. The following ten enzymes were analyzed for electrophoretically detectable genetic variation: aconitase (ACN; E.C. 4.2.1.3), aldolase (ALD; E.C. 4.1.2.13), aspartate aminotransferase (AAT; E.C. 2.6.1.1), endopeptidase (ENP; E.C. 3.4.-.-), glucose-6-phosphate dehydrogenase (GPD; E.C. 1.1.1.49), malic enzyme (ME; E.C. 1.1.1.40), phosphoglucose isomerase (PGI; E.C. 5.3.1.9), phosphoglucomutase (PGM; E.C. 5.4.2.2); superoxide dismutase (SOD; E.C. 1.15.1.1) and triosephosphate isomerase (TPI; E.C. 5.3.1.1). Electrophoretic procedures followed the general methodology of Wendel and Weeden (1989). Enzymes were extracted in cold tris-HCl buffer (Soltis et al. 1983) and resolved in 12.0% horizontal starch gels at 4°C. Three gel/electrode buffer combinations were used: AAT, ALD, ENP, ME, PGI, SOD, and TPI were examined in a pH 8.3 lithium-borate/tris-citrate system; GPD and PGM were examined in a pH 5.7 histidine-citrate system; and ACN was examined in a pH 6.1 morpholine citrate system. Enzyme/buffer combinations which provided high activity, clear bands, and consistent results were selected. Enzyme activity was assayed following the protocols of Wendel and Weeden (1989) and photographed with color print film.

Multiple loci for an enzyme were numbered sequentially with the most anodally migrating isozyme designated "1". Likewise, enzyme variants at a locus were given letters with the fastest allozyme designated "a". Standard measures of genetic polymorphism (Tables 1, 2, and 3) were calculated by hand or with Genestat-PC 3.3 (Lewis 1993). The calculation of expected heterozygosity (H_e) was unbiased for sample size (Nei 1987). This program was also used to calculate Nei's genetic identity (I) unbiased for sample size (Nei 1978) for all pair-wise sample comparisons and Nei's (1973) gene diversity statistics (H_T , H_S , and G_{ST}), unbiased for sample size and population

TABLE 2. ALLOZYME VARIATION AND MEASURES OF GENETIC DIVERSITY AT THE SUBPOPULATION LEVEL IN KINCAID'S AND SPUR LUPINE (*L. arbustus*) AT BASKETT BUTTE. Legend as in Table 1. Significant deviations ($P < 0.05$) from Hardy-Weinberg expectations are marked by an asterisk.

Abbreviation	Taxon	Location	Fender's Blue	<i>N</i>	<i>P</i> (%)	<i>A_p</i>	<i>H_o</i>	<i>H_u</i>	<i>F</i>
BB-kin-1	<i>kincaidii</i>	butte top	present	15.1	26.7	2.00	0.251	0.139	-1.000*
BB-kin-2	<i>kincaidii</i>	southwest base	present	9.5	26.7	2.00	0.289	0.140	-1.000*
BB-int	<i>kincaidii</i> × <i>arbustus</i>	southwest slope	present	6.8	33.3	2.20	0.186	0.151	-0.324
BB-arb-1	<i>arbustus</i>	butte top	present	14.5	40.0	2.50	0.138	0.180	0.204
BB-arb-2	<i>arbustus</i>	north meadow	present	13.9	46.7	2.43	0.177	0.179	0.078

TABLE 3. GENETIC POLYMORPHISM AND GENE DIVERSITY STATISTICS (NEI 1973) AT THE SPECIES LEVEL FOR *LUPINUS SULPHUREUS* SSP. *KINCAIDI* AND OTHER SPECIES WITH SIMILAR CHARACTERISTICS (HAMRICK AND GODT 1990). P_s = Percentage of polymorphic loci; A_s = average number of alleles per locus; A_{es} = effective number of alleles per locus; H_{es} = total gene diversity, averaged over all loci; H_{ET} = total gene diversity; H_{es} = gene diversity within populations; G_{ST} = the proportion of total gene diversity found among populations. Estimates of H_{ET} and H_{es} are biased for sample size and population number, and include polymorphic loci only. For unbiased estimates (Nei 1973), see text. The number of taxa included in each category is given separately for P_s , A_s , A_{es} , H_{es} (N_{pol}) and H_{ET} , H_{es} , G_{ST} (N_{div}). Standard errors are in parentheses.

Categories	N_{pol}	P_s	A_s	A_{es}	H_{es}	N_{div}	H_{ET}	H_{es}	G_{ST}
<i>L. kincaidii</i>									
long-lived perennial herb	4	46.7	1.67	1.22	0.123		0.264	0.231	0.119
		39.6	1.42	1.28	0.205	2	0.346	0.282	0.213
	(16.5)	(0.13)	(0.12)	(0.084)	(0.018)	(0.018)	(0.024)	(0.024)	(0.144)
short-lived perennial herb	152	41.3	1.70	1.15	0.116	119	0.300	0.222	0.233
		(2.2)	(0.06)	(0.01)	(0.009)		(0.013)	(0.013)	(0.019)
narrow distribution	101	45.1	1.83	1.17	0.137	82	0.300	0.215	0.242
		(2.8)	(1.17)	(0.02)	(0.011)	(0.015)	(0.015)	(0.013)	(0.024)
outcrossing, animal	172	50.1	1.99	1.24	0.167	124	0.310	0.243	0.197
		(2.0)	(0.07)	(0.02)	(0.010)	(0.010)	(0.010)	(0.010)	(0.017)

number. In addition, biased gene diversity statistics (H_{ET} and H_{ES}) were calculated for polymorphic loci only in order to facilitate comparison with the summary values of Hamrick and Godt (1989). All loci were included in the calculation of G_{ST} , as this results in the same value as excluding them (Lewis 1993).

The fixation index ($F = 1 - H_o/H_e$, where H_o is observed heterozygosity and H_e is expected heterozygosity) measures deviations from Hardy-Weinberg equilibrium and was calculated for polymorphic loci within each population (Wright 1965). Negative values indicate an excess of heterozygotes, and positive values a deficiency. A chi-square test was used to measure significant deviations from the expected value ($F = 0$). Estimates of interpopulational gene flow (number of migrants per generation, Nm) were calculated for eight populations of Kincaid's lupine (excluding Baskett Butte). The value of Nm was calculated using two methods as described in Godt and Hamrick (1993). The method of Wright (1978) as modified by Crow and Aoki (1984) is based on the coefficient of gene differentiation (G_{ST}). The method of Slatkin (1985) is based on the frequency of "private" alleles restricted to a single population.

RESULTS

Fifteen putative loci with 28 alleles (numbers in parentheses) were resolved: *Aat-1* (4), *Acn-1* (3), *Ald-1* (1), *Enp-1* (2), *Gpd-1* (2), *Me-1* (1), *Pgi-1* (1), *Pgi-2* (4), *Pgm-1* (1), *Pgm-2* (1), *Pgm-3* (2), *Sod-1* (1), *Tpi-1* (1), *Tpi-2* (2), and *Tpi-3* (2). The complete data set is available from the authors upon request. Measures of genetic polymorphism at the population and subpopulation level are summarized in Tables 1 and 2. Since population samples were generally small, the measures of genetic polymorphism presented below have relatively high standard errors associated with them. For this reason, the results are interpreted conservatively.

The Baskett Butte subpopulations assigned to *L. s. kincaidii* were treated separately due to the complicating effects of fixed heterozygosity (see below). The eight remaining populations of *L. s. kincaidii* had a percentage of polymorphic loci (P) ranging from 13.3% to 40.0% (Table 1). The average number of alleles at a polymorphic locus (A_p) ranged from 2.2 to 2.5. Observed heterozygosity (H_o) averaged 0.134 and ranged from 0.078 to 0.153. Values of unbiased expected heterozygosity (H_u) averaged 0.111 and ranged from 0.070 to 0.146. The mean fixation index over these eight populations of Kincaid's lupine was $F = -0.115$ and ranged from 0.063 to -0.301. None of these values were significantly different from the expectations of Hardy-Weinberg equilibrium.

Gene diversity statistics (Nei 1973; Hamrick and Godt 1989) and measures of genetic polymorphism at the species level are sum-

marized in Table 3. Estimates of H_{ET} and H_{ES} (excluding polymorphic loci and variation in sample number and population size) were 0.264 and 0.231, respectively. The unbiased estimate of total gene diversity over all loci (H_T) equalled 0.126, and the majority of gene diversity was distributed within populations ($H_S = 0.111$). On average, only 11.9% of the genetic variation resided among populations ($G_{ST} = 0.119$). Calculating interpopulational gene flow Nm with the unbiased estimate of G_{ST} resulted in $Nm = 0.843$. Two private alleles (both in the Hillaire Road population) at a mean frequency of 0.033 resulted in an estimate of $Nm = 3.92$.

The distribution of genetic diversity within a population was measured at the McDonald Forest site (Table 1). Nei's genetic identity between the two subpopulations was 0.995. Two alleles (*Pgi-2c* and *Pgm-3b*) with a mean frequency of 0.063 were present in the lower and absent in the upper subpopulation. A total of 4.9% of the genetic variation was distributed between the subpopulations ($G_{ST} = 0.049$). The number of migrants per generation (Nm) as estimated with G_{ST} was 1.03 and with private alleles, $Nm = 1.14$.

The mean genetic identity value between the two subpopulations of *L. arbustus* (BB-arb-1 and BB-arb-2) and the eight allopatric populations of *L. s. kincaidii* was $I = 0.947$ (Table 4). These two subpopulations of *L. arbustus* possess four alleles (*Aat-1a* [0.211], *Enp-1b* [0.378], *Pgi-2a* [0.276], *Pgm-3b* [0.104]) absent in allopatric *L. s. kincaidii*. In addition, two alleles were present at a relatively higher mean frequency in *L. arbustus* than in allopatric *L. s. kincaidii* (*Acn-1a*, 0.388 vs. 0.100; *Gpd-1b*, 0.530 vs. 0.111). Five of these six alleles (excluding *Pgm-3b*) were also found in the morphologically intermediate subpopulation (BB-int), and one locus exhibited the fixed heterozygote pattern *Acn-1a/b*. One of these six alleles (*Pgm-3b*) was found in one of the Baskett Butte subpopulations considered to represent Kincaid's lupine (BB-kin-1); and one allele was found in the other subpopulation (*Gpd-1b* in BB-kin-2). Thus all three Baskett Butte subpopulations considered to represent Kincaid's lupine or intermediates had some of the characteristic alleles of spur lupine.

A fixation index of -1.00 ($P < 0.05$) was observed in BB-kin-1 and BB-kin-2 (Table 2). This result reflects the fixed heterozygosity at four loci in each population. Three of these fixed heterozygote patterns were shared by BB-kin-1 and BB-kin-2 (*Aat-1b/c*, *Acn-1b/c*, *Pgi-2b/c*). The heterozygote *Pgm-3a/b* was found in all individuals of BB-kin-1; *Gpd-1a/b* was found in all BB-kin-2 individuals. Fixed heterozygosity was not observed in populations of *L. s. kincaidii* outside of Baskett Butte.

The two subpopulations of spur lupine had a higher percentage of polymorphic loci and more alleles per polymorphic locus than nearly all of the Kincaid's lupine populations (Tables 1 and 2).

TABLE 4. NEI'S GENETIC IDENTITY, UNBIASED FOR SAMPLE SIZE (1978). Mean values for between and within group comparisons are given. N = number of samples. Eight populations of Kincaid's lupine (excluding Baskett Butte) are included under "Kincaid's" and the range of genetic identity values is given for their 36 pairwise comparisons.

Taxon	N	BB-kin	BB-int	BB-arb	Kincaid's
BB-kin	2	0.968	0.928	0.935	0.986
BB-int	1		1.000	0.972	0.930
BB-arb	2			0.968	0.947
Kincaid's	8				0.984 (0.954–1.000)

Positive values of the fixation index were observed in the two subpopulations of spur lupine (Table 2); however these were not significantly different from the expectations of Hardy-Weinberg equilibrium.

DISCUSSION

Levels and distribution of genetic variability in Kincaid's lupine. Hamrick and Godt (1989) have summarized the patterns of allozyme variation found in 653 studies representing 449 plant species. The levels of genetic polymorphism in Kincaid's lupine as measured by percentage of polymorphic loci (P_S), average number of alleles per locus (A_S), effective number of alleles per locus (A_{es}), and total gene diversity over all loci (H_{es}), are generally similar to those found in short-lived perennial herbs, species with a narrow geographic distribution, and animal-pollinated species (Table 3). Kincaid's lupine is a long-lived perennial, but comparisons to this category are inconclusive, since the summary is based on only four studies vs. 152 for short-lived perennial herbs (Table 3, Hamrick and Godt 1989).

Although the levels of genetic variation observed in Kincaid's lupine are near the mean for species with similar growth form, breeding system, and geographic distributions, it does have a lower value of G_{ST} than comparable species (Table 3, Hamrick and Godt 1989). The fact that only 11.9% of the observed genetic variation resides among populations is reflective of a relatively low level of population differentiation. Similarly the mean genetic identity of Kincaid's lupine populations ($I = 0.984$) is relatively high for conspecific plant populations (Crawford 1989).

Low values of G_{ST} and high interpopulational I are characteristic of species with significant gene flow among populations. However, the estimated level of gene flow based on G_{ST} is only $Nm = 0.843$. For neutral genes, Nm needs to be greater than one to prevent divergence due to genetic drift (Wright 1978). Although a higher value of Nm is estimated using private alleles ($Nm = 3.92$), the fact that this method can be inaccurate when population sizes and the number

of rare alleles are low (Slatkin and Barton 1989) leads us to prefer the first estimate. Due to its fragmented distribution, actual gene flow between the disjunct populations of Kincaid's lupine is presently unlikely. However, populations may have been distributed continuously in the past (as recently as 150 years ago), providing opportunities for gene flow and explaining the low levels of genetic differentiation and high genetic identities among populations.

The levels of genetic variation observed between populations with and without Fender's Blue did not substantially differ (Table 1). For example, the two populations with the highest (Hillaire Road) and lowest (Boistfort Cemetery) number of polymorphic loci did not host Fender's blue. Among populations which do host the butterfly, McDonald Forest, Willow Creek, and Oak Ridge had the highest number of polymorphic loci. Within-population differentiation at McDonald Forest was observed (Table 1). The lower McDonald Forest subpopulation has two alleles not observed in the upper subpopulation. Although suggestive of differentiation, these results could also be attributed to sampling error resulting from the relatively small subpopulation sizes.

Seven of the eight allopatric populations of Kincaid's lupine had positive values of F , the fixation index (Table 1). However no population had a value of F significantly different from zero, suggesting that the populations can be considered to be in Hardy-Weinberg equilibrium. This is indicative of an outcrossing breeding system, and is consistent with the observed self-incompatibility in Kincaid's lupine (Kuykendall and Kaye 1993). The two subpopulations of spur lupine had negative (but not significantly different from zero) values of F . The consistent (but non-significant) differences in the direction of the deviations from Hardy-Weinberg equilibrium may be indicative of differing breeding systems in the two species.

Evidence for hybridization on Baskett Butte. Spur lupine (*L. arbuscus*) and Kincaid's lupine are generally allopatric. The two species have a mean genetic identity of $I = 0.947$, and no fixed allelic differences (alternate alleles at a frequency of $P = 1.00$) separate the two. However four spur lupine alleles at average frequencies of 0.146–0.378 are absent in Kincaid's lupine, while two additional loci are present at high frequency in spur lupine (0.388 and 0.530) and low frequency (0.100 and 0.111) in Kincaid's. These six alleles can be used to document introgression between the two species. On Baskett Butte, where the two species are sympatric, all surveyed individuals considered to represent Kincaid's lupine or intermediates had some of the alleles characteristic to spur lupine.

Hybridization and introgression are very widespread phenomena in the genus *Lupinus* (Phillips 1957), and it is possible that the high genetic identity observed between Kincaid's and spur lupine may be a consequence of past genetic interchange. Likewise, the relatively

high levels of genetic diversity in spur lupine on Baskett Butte may have resulted from past introgression with Kincaid's lupine or other species. Additional allopatric populations of spur lupine would need to be examined in order to confirm this hypothesis.

Considering the high frequency of hybridization in the genus, it is not surprising that individuals suggestive of a hybrid origin were identified prior to the isozyme study. The subpopulation (BB-int) comprised of seven morphologically intermediate individuals has all four alleles that are restricted to spur lupine. Interestingly, all seven individuals exhibit the heterozygous pattern *Acn-1a/b*. Unfortunately, the ploidy level of these individuals is unknown. Thus it cannot be determined if this "fixed heterozygosity" is the result of two loci in a hybrid tetraploid or allelic heterozygosity.

The genetic situation found in the two subpopulations considered to represent Kincaid's lupine (BB-kin-1 and BB-kin-2) is rather different. Within each subpopulation, individuals are identical at the sampled loci and have fixed heterozygote patterns at four loci. This "heterozygote excess" results in values of $F = -1.00$ ($P < 0.05$) in these two subpopulations. The only difference between the two subpopulations is that one of the fixed heterozygote genotypes within BB-kin-1 is *Pgm-3a/b* while BB-kin-2 has *Gpd-1a/b*. It is at these latter two loci that each population has one of the characteristic alleles of spur lupine (*Pgm-3b* and *Gpd-1b*). The simplest explanation for the uniform genotypes in each subpopulation is that the "individuals" sampled in BB-kin-1 and BB-kin-2 are actually ramets of large vegetative clones. Furthermore, each clone must have had an independent origin due to the different fixed heterozygote genotypes at PGM and GPD. It is likely that each clone resulted from a separate hybridization event between spur and Kincaid's lupine. Observations of BB-kin-1 over four years (A. Liston unpublished data) suggest that this "individual" is sterile. The majority of the ramets do not produce inflorescences, and there is no evidence that flowering ramets produce seed. Pollen viability in these individuals is low as measured by lactophenol staining (K. St. Hilaire unpublished data). Other populations of Kincaid's lupine show high viability (nearly 100% pollen staining, K. St. Hilaire unpublished data).

Wolko and Weeden (1989) tested ten enzyme systems in five *Lupinus* species and found duplicate isozyme expression at 2–7 loci within individuals from each species. These data were interpreted as consistent with an ancient tetraploid origin of the *Lupinus* genome (Wolko and Weeden 1989). In Kincaid's and spur lupine three loci were observed for PGM and TPI (two are expected in diploid plants, Weeden and Wendel 1989). Thus duplicate gene expression is found in only two of the ten surveyed enzyme systems, suggesting that although these species are cytologically tetraploid, their genome is effectively diploidized (Wolko and Weeden 1989).

Duplicate gene expression (fixed heterozygosity) at four loci in

BB-kin-1 and BB-kin-2 suggests that these plants have a higher ploidy level than spur lupine and allopatric Kincaid's lupine. Both $n=24$ "tetraploids" and $n=48$ "octoploids" have been reported from spur lupine (as *L. laxiflorus*) (Phillips 1957). Thus it is predicted that BB-kin-1 and BB-kin-2 are $n=48$. Cytological confirmation of the inferred ploidy level of these clones would provide further evidence for their putative hybrid origin. In addition, the total extent of each clone could be determined by the genotyping of all putative ramets in the subpopulations.

Management implications. The relatively low level of genetic differentiation among populations of Kincaid's lupine suggests that only normal precautions need to be taken in choosing seed sources used in revegetation of native prairie. Thus while seeds from a nearby source are preferable, geographic differentiation does not appear to be significant in Kincaid's lupine. Since populations with and without Fender's blue are undifferentiated, it might be desirable to collect seeds in non-host populations in order not to risk impacting the butterfly. It would also be desirable to collect seeds from populations with the highest levels of observed diversity.

Despite evidence of hybridization between Kincaid's lupine and spur lupine on Baskett Butte, this does not appear to pose a threat to the survival of the endangered Fender's blue butterfly. In fact, the sterile clones of presumed hybrid origin are used by the butterfly for oviposition (A. Liston unpublished observation). Hybridization between a rare plant and a widespread congener can be considered a threat to the "genetic integrity" of the rare plant (Rieseberg 1991). In some cases, it has even been suggested that the widespread species be physically removed from the site of a rare species (Rieseberg et al. 1989). However, the fact that no "pure" Kincaid's lupine individuals were found on Baskett Butte suggests that such manipulation would be impossible in this situation.

Although spur lupine is widespread in central Oregon, it is only known from two additional sites in the Willamette Valley. Preliminary isozyme results also suggest that spur lupine from Baskett Butte is genetically isolated from central Oregon populations (K. St. Hilaire and A. Liston unpublished data). Spur lupine serves as an alternative host of Fender's blue, and on Baskett Butte supports the largest known population of the butterfly (Hammond and Wilson 1993). Thus although conservation efforts have focused on Kincaid's lupine, spur lupine in the Willamette Valley is also deserving of protection.

ACKNOWLEDGMENTS

Support for this research was generously provided by the "Partners in Science Program" of the M.J. Murdock Charitable Trust of Research Corporation. We also

thank Norman Weeden for reviewing the manuscript, Paul Hammond and Kenton Chambers for advice and assistance, Tom Kaye and Keli Kuykendall for unpublished observations, and Maura Naughton of the U.S. Fish and Wildlife Service for permission to work at Baskett Slough National Wildlife Refuge.

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(Received 16 Aug 1994; accepted 9 Dec 1994)

MONOECIOUS MORPHS IN *CROTON CALIFORNICUS* (EUPHORBIACEAE)

BRADFORD D. MARTIN

Department of Biology, La Sierra University,
Riverside, CA 92515

ABSTRACT

Croton californicus is reported to be a dioecious plant species. Monoecious morphs were observed in five populations in southern California. The prevalence of monoecious individuals was low with a total relative abundance of 2.2%. Female plants were more numerous than male plants in four of the five populations with a total male:female sex ratio of 0.90. Male plants were significantly larger than female plants for crown diameter and plant height while monoecious morphs did not differ significantly.

Croton californicus Muell. Arg. is a subshrub that inhabits sandy soils, dunes, and washes below 900 m in various plant communities of California, Arizona, and Baja California. It is reported to be a dioecious species (Webster 1993). Female plants bear small, whitish pistillate flowers with twice forked styles that resemble staminate flowers on male plants. The present study has noted monoecious morphs (Fig. 1) in several populations of southern California. It appears that *C. californicus* is currently in a diclinous condition other than dioecy proper. The purpose of this study was to document the occurrence and prevalence of monoecious individuals in several populations of *C. californicus*. Since most studies of dioecy have focused on temperate herbs (Ornduff 1981), the study of this subshrub should increase our incomplete understanding of sexual systems in woody plants and the evolution of plant breeding systems in general (Willson 1983).

METHODS

Measurements of *Croton californicus* were performed in five populations of southern California (Fig. 2). Populations at Loma Linda and California State University San Bernardino (CSUSB) were located in sandy soils of coastal sage scrub communities. The Loma Linda population was associated with *Encelia farinosa* Torrey & A. Gray, *Salvia mellifera* E. Greene, *Artemisia californica* Less., *Rhus trilobata* Torrey & A. Gray, *KeckIELLA antirrhinoides* (Benth.) Straw, and *Lepidospartum squamatum* (A. Gray) A. Gray. The CSUSB population was associated with *S. mellifera*, *A. californica*, *A. dracunculus* L., *Eriogonum fasciculatum* Benth., and *Marrubium vul-*



FIG. 1. A monoecious morph of *Croton californicus* exhibiting (from left to right) a fruit, a pistillate flower, and a staminate flower adjacent to one another.

gare L. *Croton* populations at Rubidoux, San Bernardino, and Redlands were located in sandy soils of the Santa Ana River floodplain. The Rubidoux population was associated with *Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers., *Urtica dioica* L. and *M. vulgare*. The San Bernardino population was associated with *B. salicifolia*, *L. squamatum*, *M. vulgare*, and the endangered *Eriastrum densifolium* ssp. *sanctorum* (Milliken) H. Mason. The Redlands population was associated with *Juniperus californica* Carriere, *E. densifolium* ssp. *sanctorum*, *E. fasciculatum*, *Eriodictyon trichocalyx* A. A. Heller, *Gutierrezia californica* (DC.) Torrey & A. Gray, *L. squamatum*, *Opuntia parryi* Engelm., *O. littoralis* (Engelm.) Cockerell, and *Yucca whipplei* Torrey.

The flowering season for *C. californicus* extends from March to October (Munz 1974). All flowering individuals in each population

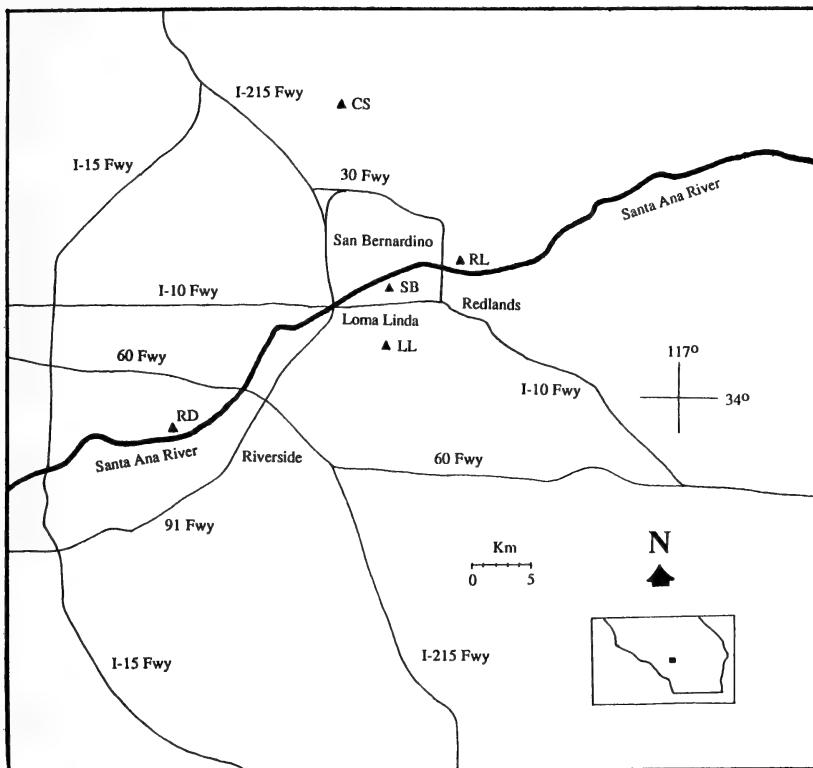


FIG. 2. Map of the study area. Study populations of *Croton californicus* are indicated by triangles. RD = Rubidoux; LL = Loma Linda; CS = California State University San Bernardino; SB = San Bernardino; RL = Redlands.

were examined near the end of the flowering season at Rubidoux, Loma Linda, and CSUSB on 3 October 1984, 7 October 1984, and 2 October 1985 respectively. Sexual condition was recorded and plant crown diameter, plant height, and leaf blade length were recorded for all the sexed plants or randomly recorded for many of the sexed plants. Sexual condition was determined by examining all of the flowers on a plant and by the presence or absence of fruits. Monoecious morphs were determined to be plants that bore both pistillate and staminate flowers. Leaf blade length was determined by sampling the largest leaf on each plant.

Samples of *Croton* populations in San Bernardino and Redlands were measured on 16 October 1991 and 23 October 1991 respectively. Plot sampling, using 1 m² quadrats, was performed in these two populations to determine population density, cover, and frequency as well as to record sexual condition and plant crown diameter. Cover was calculated from plant crown diameters. Although

TABLE 1. RELATIVE ABUNDANCE (%) FOR SEXUAL MORPHS OF *CROTON CALIFORNICUS* IN FIVE POPULATIONS OF SOUTHERN CALIFORNIA.

Population	Relative abundance						Male : female ratio	
	Female		Male		Monoecious			
	n	%	n	%	n	%		
Rubidoux	121	55.5	95	43.6	2	0.9	0.79	
Loma Linda	108	45.0	123	51.3	9	3.7	1.14	
CSUSB	128	53.3	109	45.4	3	1.3	0.85	
San Bernardino	55	53.9	43	42.2	4	3.9	0.78	
Redlands	31	50.0	30	48.4	1	1.6	0.97	
Total =	443	51.4	400	46.4	19	2.2	0.90	

nonflowering plants and seedlings were also recorded, sexual condition could not be determined for these plants. Seedlings were designated as plants with crown diameters of less than 5 cm. Two hundred 1 m² quadrats were randomly sampled in each of these populations.

Statistical comparisons were made between sexual conditions and morphological data for all *Croton* populations using one-way ANOVA. Two-way ANOVA was also performed to analyze within and between population differences. Linear correlation was used to analyze the relationship of plant crown diameter with plant height.

RESULTS

Monoecious morphs of *Croton californicus* were present in all five of the study populations (Table 1). Relative abundance of monoecious morphs was low with a total relative abundance of 2.2% and values ranging from 0.9–3.9% for the different populations. Females were more numerous than males in all populations with the exception of Loma Linda. Male:female sex ratios ranged from 0.78–1.14 in the various populations with the total male:female ratio being 0.90.

Male plants of *C. californicus* were found to be larger when compared to female plants (Table 2). Male crown diameter was larger in all populations and significantly larger ($P < 0.05$) in three of the five populations. Male plant height was significantly higher ($P < 0.01$ or $P < 0.05$) than female plant height in two of the three populations measured. Totals for crown diameter and plant height also reflect that male plants were significantly larger ($P < 0.01$ or $P < 0.05$) than female plants. Monoecious morphs were not significantly different in size for crown diameter or plant height when compared to females or males in all populations. Crown diameter was correlated positively ($r = +0.775$, $+0.788$, and $+0.725$) with plant height for females, males, and monoecious morphs respec-

TABLE 2. MORPHOLOGICAL CHARACTERS (MEAN \pm SD) FOR SEXUAL MORPHS OF *CROTON CALIFORNICUS* IN FIVE POPULATIONS OF SOUTHERN CALIFORNIA. All units are in cm. Sample sizes are numbers in parentheses (n). RD = Rubidoux; LL = Loma Linda; CS = CSUSB; SB = San Bernardino; RL = Redlands. * = $P < 0.05$. ** = $P < 0.01$. There were significant differences ($P < 0.01$) among populations for crown diameter and plant height means.

Popula- tion	Crown diameter						Morphological characters					
	Female			Male			Monoe- cious			Plant height		
	Female	Male		Female	Male		Female	Male		Female	Male	Leaf blade length
RD	66.0 \pm 33.1*	75.0 \pm 31.0*		43.0 \pm 38.2	58.1 \pm 18.0**		65.3 \pm 20.5**	43.0 \pm 26.9		3.1 \pm 0.8	3.1 \pm 0.9	2.7 \pm 0.3
LL	(121)	(95)	(2)	(121)	(95)	(2)	(121)	(95)	(2)	(121)	(95)	(2)
CS	40.1 \pm 16.3	42.9 \pm 19.2		38.0 \pm 20.2	34.2 \pm 9.4		33.7 \pm 9.7	37.7 \pm 13.3		3.3 \pm 0.6	3.2 \pm 0.7	3.8 \pm 0.6
SB	28.6 \pm 14.3*	36.6 \pm 16.6*		45.3 \pm 31.6	—		(57)	(3)	(57)	(62)	(57)	(3)
RL	37.7 \pm 16.0	44.8 \pm 18.9		82.0	—		—	—	—	—	—	—
Total =	47.6 \pm 29.1**	55.0 \pm 29.5**		53.0 \pm 26.6	49.6 \pm 18.6*		53.6 \pm 21.3*	48.2 \pm 14.9		3.1 \pm 0.7	3.0 \pm 0.8	2.8 \pm 0.8
	(323)	(285)	(19)	(237)	(19)	(1)	(214)	(14)	(237)	(14)	(237)	(14)

TABLE 3. DENSITY, COVER, AND FREQUENCY OF *CROTON CALIFORNICUS* IN TWO POPULATIONS OF SOUTHERN CALIFORNIA. Cover was calculated from plant crown diameters. K = number of 1 m² quadrats sampled.

Population	Phenological condition	Density (no./ha)	Cover (%)	Frequency (%)
San Bernardino (K = 200)	Flowering	5100	5.34	32.5
	Nonflowering	650	0.13	5.5
	Seedling	800	0.01	5.0
	Total =	6550	5.48	36.5
Redlands (K = 200)	Flowering	3100	5.07	24.0
	Nonflowering	350	0.14	3.5
	Seedling	100	<0.01	1.0
	Total =	3550	5.21	26.5

tively. There were significant interpopulational differences ($P < 0.01$) for crown diameter and plant height.

Density, cover, and frequency data for two populations of *C. californicus* is presented in Table 3. Density and frequency were higher in the San Bernardino population when compared to the Redlands population. Cover values are relatively close between populations with 5.48% in San Bernardino and 5.21% in Redlands. Both populations contained a considerable number of plants that were not flowering. Nonflowering plants and seedlings composed 22.1% and 12.7% of the plants sampled in the San Bernardino and Redlands populations respectively. Seedlings were more numerous than non-flowering plants in the San Bernardino population while the reverse was observed in the Redlands population. Many of the nonflowering plants in both populations were as large or larger than some of the flowering plants.

DISCUSSION

Although the frequency of monoecious morphs observed in this study was low, the occurrence of these morphs in populations of *Croton californicus* appears to be widespread in southern California. Many dioecious species are known to have populations with hermaphrodites at low frequencies (Charlesworth and Charlesworth 1978; Willson 1983; Bullock 1985) and there exist many intergrades between the various sexual systems of plants (Willson 1983; Bullock 1985). Bullock (1985) noted variable sex expression in some dioecious species of a tropical deciduous forest in Jalisco, Mexico, particularly in *Jatropha* and *Bernardia* of the Euphorbiaceae. Male plants vary in the tendency to produce a single female flower at the base of the inflorescence. The genus *Croton* is interesting for its diversity at this same locality: monoecy typifies most species, but the ratio of male to female flowers varies widely, and two species

consist of monoecious and female individuals; two species are dioecious (Bullock 1985; Tejada and Bullock 1988).

Unfortunately, the proportion of male to female flowers on monoecious plants was not quantified in this study. It was noted during data collection that on many monoecious individuals whole branches bearing pistillate or staminate racemes were situated on plants predominantly of the opposite sex. However, there were some monoecious plants that had several branches that were a mixture of both pistillate and staminate flowers. Often times pistillate and staminate flowers were situated alternate and adjacent (Fig. 1) to each other on the same raceme. One monoecious morph in the CSUSB population was noted to have one hermaphroditic flower as well as pistillate and staminate flowers. Three monoecious plants in the Loma Linda population were located within 1 m of each other. Close proximity of monoecious plants to one another has been recently noted by the author in four additional populations in December 1993. Although significant size differences of monoecious plants when compared to male or female plants were not detected in this study, this may be due to the small sample size ($n = 19$).

Vegetative parts of female and male *Croton* plants are morphologically identical which makes identification of the sexes impossible without flowers being present. This study observed size to be a secondary sex character in which males are larger than females. Most secondary sex characters of plants are subtle and usually are expressed in terms of growth, resource allocation, and timing or longevity (Richards 1986). Female biased sex ratios, as observed in this study, are rarer in nature than male biased sex ratios (Willson 1983; Richards 1986). The sex ratio in plant populations may not be equal due to microhabitat segregation by the different sexes (Handel 1983). There is some evidence in subdioecious species that females are relatively constant in their sex expression and it is the polleniferous plants which are variable (Heslop-Harrison 1957; Charlesworth and Charlesworth 1978). This may be true with *C. californicus* because when male and monoecious plants are added together, the male:female ratio is closer to 1.00.

Cover values of *C. californicus* in this study were similar to those found by Zembal and Kramer (1984). They found *C. californicus* closely associated with the endangered *Eriastrum densifolium* ssp. *sanctorum* in five out of six study populations. Cover values ranged from 0.3–5.8%, however, density values were lower than the current study. The immaturity of seedling plants in the present study did not allow many individuals in each population to be sexed. However, the nonflowering condition of the large number of plants in this study appears to be due to some factor other than immaturity. Possibly some of these plants were situated in drier locations and ceased flowering due to physiological stress.

Although monoecious individuals compose only a small fraction of a given population, their presence suggests that *C. californicus* may have an unusual breeding system. Three possibilities could explain the occurrence of the three sexual morphs. First, *C. californicus* may be a sequential hermaphroditic species that at any one time contains a small percentage of individuals undergoing sex reversal. If size determines when an individual switches sex, then we might expect the larger and most vigorous plants to be female (Willson 1983). This study observed that male plants were larger than female plants. Large male plants appeared to be healthy, vigorous, and not in any way senescent. There are several examples of dioecious species where the males are larger, taller, and/or more vigorous than the females (Willson 1983; Richards 1986). Longitudinal field studies are needed (Ornduff 1981) to monitor individual plants for one to several seasons to observe if sex reversal is occurring. Quantifying the number of pistillate and/or staminate flowers through time is necessary to reveal the femaleness or maleness of each individual plant.

Second, *C. californicus* may be in a subdioecious condition whereby some individuals exhibit phenotypic volatility for sex expression due to environmental influence. Phenotypic plasticity is well known (Willson 1983), and Heslop-Harrison (1957) cites many examples of plant intersexuality (a transformation from a normal condition of unisexuality to complete or partial bisexuality). Experiments are needed in which plants are subjected to changes in various environmental conditions such as light intensity, photoperiod, temperature, moisture, and pruning to see if sex expression is environmentally influenced (Heslop-Harrison 1957; Cleland and Ben-Tal 1981; Richards 1986). Also, experiments involving applications of various nutrients and plant growth substances such as nitrogen, auxin, ethylene, GA, cytokinins, and maleic hydrazide may reveal if there is any hormonal control of sex expression (Heslop-Harrison 1957; Cleland and Ben-Tal 1981; Richards 1986).

Third, *C. californicus* may be in a subdioecious condition whereby the three sexual morphs are genetically fixed. Genetic experiments, such as pollination between male and female plants, male and monoecious plants, monoecious and female plants, and monoecious and monoecious plants, are needed to reveal any relationship between genetics and sex expression.

The present study indicates that the second or third possibilities of a subdioecious sexual condition in *C. californicus* are more likely than the possibility of sequential hermaphroditism. Subdioecy represents a stage in the evolution from monoecy to dioecy or vice versa. It is likely that dioecy has evolved from monoecy on several occasions (Charlesworth and Charlesworth 1978; Ross 1982). Both

genotypic or phenotypic subdioecious conditions may reflect an evolutionary step for *C. californicus* from monoecy to dioecy.

ACKNOWLEDGMENTS

I thank Bill Khoury, Nalorn Sengamphan, Ernie Schwab, Gary Bradley and Norman Mitchell for their assistance with this study and manuscript.

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(Received 5 Apr 1994; accepted 20 Oct 1994)

DEMOGRAPHIC STUDY OF THE RARE
CORYPHANTHA ROBBINSORUM (CACTACEAE) IN
SOUTHEASTERN ARIZONA

ROBERT J. SCHMALZEL
Oracle, AZ

FRANK W. REICHENBACHER*
Southwestern Field Biologists
8230 E. Broadway Blvd., Suite W8 Tucson, AZ 85710-4002

SUE RUTMAN
U.S. Fish and Wildlife Service
3616 W. Thomas Rd., Suite 6 Phoenix, AZ 85019

ABSTRACT

Growth, fecundity and demography of the cactus *Coryphantha robbinsorum* are described based on a five year study of three permanent plots in Cochise County, Arizona. Four size stages were recognized: seeds, juveniles \leq 11 mm diameter (J1), juveniles $>$ 11 mm diameter (J2), and adults (A). Mean numbers of plants per year per meter² were 1.11 in Plots A and C, and 0.70 in Plot B. The number of flowers and fruits produced annually by each adult was determined. The smallest plants to flower (become adults) were 13 mm in diameter. More than half of the plants flowered upon attaining an 18 mm diameter. Large adults produced more flowers and fruits than did small adults. During the five years, over 50% of the fruit produced by the population came from 25 individuals who represented only 23% of the adult population. The average number of fruits produced annually per adult was 1.58 ± 0.89 (mean \pm 1 SD). Number of recruits to J1 was negatively correlated with total rainfall during the 12 months preceding the census. Percent survival of J1 individuals was positively correlated with winter rainfall. Neither percent mortality of J2 and adult individuals, nor fruit and flower production were significantly correlated with preceding summer, winter or annual rainfall. This cactus has a survivorship pattern with a high mortality of seeds (0.9999 individuals per year, estimated based on 33 seeds per fruit) and a decreasing mortality for each stage thereafter (J1 juveniles: 0.209; J2 juveniles: 0.054; adults: 0.027, measured). There were differences between the plots in transition and survival rates measured for the various stage classes. The finite rate of increase (λ) ranged from 1.0036 to 1.0941 for the three plots. The average λ for the 3 plots, 1.0464, predicts a doubling time for the population of about 16 years. Elasticity analysis of λ to various demographic parameters shows that, during the early 1990's adult survivorship contributed most (46–87%) to λ , J2 survivorship and the combined contribution of all growth parameters were less important than adult survivorship in their effect on λ , and fecundity and J1 survivorship were least important. A simulation experiment shows that a hypothetical increase to 50 seeds per fruit would change the average λ from 1.046 to 1.098; and a reduction to 6 seeds per fruit would change λ to 1.003. Projection of the matrix model suggests that *C. robbinsorum* is long-lived. At a stable age distribution, the mean age in the J1 stage is

* Reprint requests, comments, and questions to second author.

estimated to be 1.1–2.0 years, the J2 stage to be 3.4–5.1 years, and the adult stage to be about 17 years. The mean age of parents of offspring produced in a stable age distribution, \bar{A} , is 17.05 years.

Demographic studies require long-term monitoring of populations to obtain the information needed to assess the dynamics of a population. In a recent symposium (Sivinski and Lightfoot 1993) on Southwestern rare plants, at least 10 of the 37 papers presented the results of demographic studies. These studies developed many of the estimates of demographic parameters needed for matrix analysis, but only one of these papers (Maschinski and Rutman 1993) included matrix analyses. Matrix analysis of plant populations provides the means for determining estimates of the finite rate of increase of the population (λ) and the relative contribution of each demographic parameter to λ . This study describes the results of 5 years of demographic monitoring and matrix analysis of a population of *Coryphantha robbinsorum* (Earle) A. D. Zimmerman.

Coryphantha robbinsorum is a federally Threatened Species of cactus protected by the Endangered Species Act (Rutman 1992). This plant is restricted to limestone outcrops in an estimated area of 25 km² in the San Bernardino Valley of Cochise County, southeastern Arizona (Phillips and Brian 1982; U.S. Fish and Wildlife Service 1993) and extreme northern Sonora (Lopresti 1984). Zimmerman (personal communication to Phillips and Brian 1982) estimates that there are about 20,000 plants (\pm 10,000) of detectable size for this species. The population of *C. robbinsorum* includes plants that are scattered and plants that occur as small, isolated clusters of 100–1000 plants (U. S. Fish and Wildlife Service 1993).

We determine four demographic parameters of the *C. robbinsorum* population: establishment, mortality, growth and reproduction. These demographic parameters are then examined in relation to rainfall. Water is the major limiting factor for vegetative growth in the deserts and the productivity of arid ecosystems is highly correlated with rainfall (Noy-Meir 1973). High annual variation in establishment and growth has been noted in other cacti and succulents (Jordan and Nobel 1979, 1981; Steenbergh and Lowe 1977; Turner 1990; Johnson et al. 1993). We hypothesize that flower and fruit production are positively associated with rainfall, and mortality is negatively associated with rainfall. Also, because small plants are less able to withstand drought, we hypothesize that juveniles experience high mortality in dry years, low mortality in wet years, and that adults should be little affected by annual variation in rainfall.

A simple stage-classified life cycle graph for *Coryphantha robbinsorum* is constructed and from this life cycle graph the corresponding projection matrix (as outlined by Caswell 1986, 1989) is derived. By matrix analysis, we determine the (1) finite population growth

rate (λ), (2) the stable age distribution, and (3) mean age for each life stage of *Coryphantha robbinsorum*. We then use an elasticity matrix (Caswell 1986) to explore the relative contribution to population growth rate made by several biologically relevant parameters. In particular, we simulate alterations in four parameters to explore their effects on population growth: (1) seed bank survivorship, (2) seed to juvenile establishment rate, (3) adult mortality, and (4) fecundity.

METHODS

Plant surveys. Three circular plots, each with a 3 m radius, were established by the U.S. Fish and Wildlife Service in Cochise County, southeastern Arizona. Each plot was marked in the center with an aluminum spike and aluminum tag. Plot A was established in April 1988 at a site on a hill with a northeast exposure and a 10–20% slope. In April 1989, two more plots were established on the same hill at a site with a southwest exposure (Plot B) and at a site on top of the hill (Plot C). In each plot, every individual plant was labeled with an aluminum tag that was secured next to the plant with a nail driven into the rocky substrate. Locations are not described or shown in this report because *C. robbinsorum* is included in the Federal list of threatened species and illegal commercial harvesting is a potential threat to this cactus.

Plants were censused on 5–6 April 1988, 11 April 1989, 13 April 1989, 17–18 April 1990, 22–23 April 1991, 5 May 1992, and 19–20 April 1993. Number of flowers, fruits and width of stem(s) were recorded for each individual. Width of stem was measured with a caliper. At the time of each inventory, flowering had recently ceased. The flowers had shriveled but their remains were still present. As a result, the number of flowers as well as the number of developing fruits produced could be counted. Precipitation data were obtained from a site within 1.5 km of the study site.

Matrix analysis. We recognized four stage-classes: seeds (S), juveniles ≤ 11 mm in diameter (J1), juveniles > 11 mm in diameter (J2), and adults (A). The seed stage-class includes seedlings less than 3 mm in diameter. No seedlings less than 3 mm in diameter were found during the censuses and, for the matrix analysis, can be included in the seed stage-class. Juveniles were divided into two stage-classes because the smaller plants experienced greater rates of mortality than did the larger juveniles.

The life cycle graph for *C. robbinsorum* (Fig. 1) is directed and stage-classified, rather than age-classified. An individual in stage class i may survive and grow to stage class $i + 1$ with probability G_i , or may survive and remain in stage class i with probability P_i .

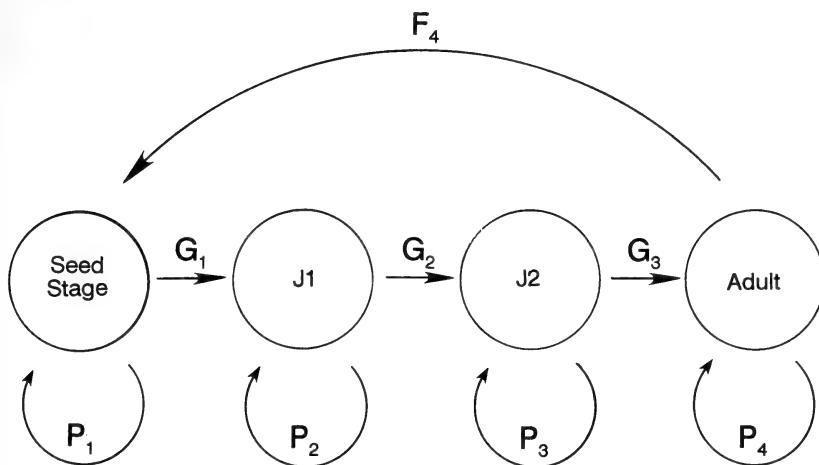


FIG. 1. Stage-classified life cycle used to depict the life cycle of *Coryphantha robustiorum*. Stage 1 = seed stage; 2 = J1 stage; 3 = J2 stage; and 4 = adult stage. F_4 = fecundity (mean number of seeds produced per plant per year) of adults. G_i is the proportion of plants in the i th stage entering the next stage, G_{i+1} . P_i is the proportion of plants remaining and surviving in the i th stage.

The illustration also indicates that an individual may not shrink or skip a stage within a single time interval. However, some plants were observed to decrease in diameter between censuses. We treated the 14 cases (out of a total of 184 J2 observations) in which a J2 shrunk to a J1 size as remaining in J2. Plants were scored as adults if there was evidence of flowering in the season of the census or if the plant had flowered during earlier censuses; nonflowering adults were still adults.

For the matrix analyses, each plot was analyzed separately. The parameters p_i and g_i used in the matrix of a particular plot were the means obtained during the five years from that plot. There was one exception to using parameter values unique to the particular plot. The same value for adult fecundity, F_4 , was used for all of the matrix analyses (except when F_4 was specifically modified). Because (1) the mean number of fruits produced per adult per year, a , was determined to be 1.6 (for all adult plants, for all five years) and (2) the average number of seeds per fruit, b , was reported to be 20 (Zimmerman 1978), F_4 was estimated to be 33; $F_4 = ab$. To determine the effect that the particular choice of our F_4 estimate had on the matrix analysis, the analyses were run using a high value (80, when $b = 50$) and a low value (9.6, when $b = 6$) for F_4 . These high and low values are very likely to bracket the actual F_4 for individuals in this population. Hildegard Nase (personal communication 1993) has harvested 2000 seeds per year for two years from 40–45 greenhouse-

$$\begin{pmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

FIG. 2. Stage-classified projection matrix used in this analysis.

grown stems of *C. robbinsorum*, or about 44–50 seeds per stem per year. In developing the matrix, the choice of mean number of seeds per fruit affects not only fecundity, F_4 , but also G_1 , the proportion of seeds becoming J1.

We did not measure P_1 , the persistence of seeds in the seed bank. Steenbergh and Lowe (1977) found that saguaros (*Carnegiea gigantea*) develop essentially no seed bank, largely due to seed predation. For the purposes of generating a very conservative analysis, we assumed that seeds remained in the seed bank for no more than one year; this assumption set P_1 at zero. We ran the general matrix analysis with P_1 set at zero, and also with P_1 set at 0.5 to determine the effect of a persistent, expanding seed bank on λ .

In order to examine the effects of changes in survival probabilities in selected life stages on λ , we altered the values for the survival probabilities of each stage, held the remaining matrix components constant, and simulated the population response. The survival probabilities in stages J1, J2 and A were modified by reducing the stage-specific annual survival by 50% and then calculating P_i and G_i using the equations of Crouse et al. (1987),

$$P_i = \frac{1 - p_i^{d-1}}{1 - p_i^d} p_i$$

and

$$G_i = \frac{p_i^d(1 - p_i)}{1 - p_i^d}$$

where d is the stage-specific mean age.

For analyzing the stage-structured transition matrix (Fig. 2), we used STAGECOACH, a program devised by Cochran and Ellner (1992).

RESULTS

Plant densities. Mean density between years of *C. robbinsorum* plants was the same on plots A and C (1.11 plants per meter² for all stages combined) (Table 1). Plot B had a lower density (0.70 plants per meter²). Significant between-year differences in numbers of individuals in all stages of Plot C were found. Also, the number

TABLE 1. NUMBER OF *C. ROBBINSORUM* PLANTS OF EACH STAGE-CLASS AND NUMBER OF FLOWERS (FL) AND FRUITS (FT) ON THE THREE STUDY PLOTS. Chi-square values of year to year variation in numbers of plants indicated as significant (*, $P < 0.005$) or not significant (NS, $P > 0.01$).

Plot	Stage	Year					Mean	P
		1989	1990	1991	1992	1993		
A	J1	23	34	29	20	22	25.6	NS
	J2	8	10	12	19	15	12.8	NS
	A	20	23	23	26	29	24.2	NS
	Fl	26	36	45	52	38	39.4	NS
	Ft	23	30	44	50	32	35.8	*
	total	51	67	64	65	66	62.6	NS
B	J1	8	6	7	5	4	6.0	NS
	J2	18	13	7	7	7	10.4	NS
	A	17	19	25	27	27	23.0	NS
	Fl	33	40	53	63	49	47.6	NS
	Ft	33	40	47	61	49	46.0	NS
	total	43	38	39	39	38	39.4	NS
C	J1	23	15	11	4	9	12.4	*
	J2	31	27	18	16	6	19.6	*
	A	14	23	34	41	43	31.0	*
	Fl	20	36	74	85	70	57.0	*
	Ft	18	29	59	76	63	49.0	*
	total	68	65	63	61	58	63.0	NS

of fruits in Plot A and flowers and fruits in Plot C varied significantly between years (Table 1).

Effect of rainfall on demographic parameters. The demographic parameters that were obtained from the yearly censuses of the three plots are presented in Table 2. Rainfall data are presented in Table 3. The period during the censuses included the driest seasons recorded for 12 years (the winter of 1989 and the summer of 1990).

Number of new J1 juveniles for all plots combined did not vary significantly among the four years ($\chi^2 = 9.73$, $P > 0.01$). Annual variation in the number of new J1 individuals was negatively correlated with total annual rainfall ($Y = 42.53 - 0.07X$, $r = -0.95$, $P < 0.01$), but was not significantly correlated with either summer ($P > 0.5$) or winter ($P > 0.5$) rainfall alone.

Percent mortality did not vary significantly among the four years for individuals in J1 ($\chi^2 = 2.2$, $P > 0.5$), J2 ($\chi^2 = 4.2$, $P > 0.1$), or A ($\chi^2 = 7.0$, $P > 0.05$) stages. However, percent survival of the J1 stage was positively correlated with winter rainfall ($Y = 70.43 + 0.05X$, $r = 0.98$, $P < 0.05$) and not significantly correlated with preceding annual ($P > 0.1$) or summer rainfall ($P > 0.5$). Percent mortality of the J2 stage was not correlated with rainfall. Percent

TABLE 2. DEMOGRAPHIC PARAMETERS OBTAINED FROM 5 CENSUSES OF THREE PERMANENT PLOTS OF *C. ROBBINSONUM* IN SOUTHEASTERN ARIZONA.

	Year				
	1990	1991	1992	1993	Mean
Number of New Individuals on Plot					
Plot A	15	10	6	3	8.5
Plot B	2	4	1	2	2.3
Plot C	5	6	2	4	4.3
Total	22	20	9	9	15.0
Mortality (pooled data from the 3 plots)					
J1	0.264	0.204	0.170	0.200	0.209
J2	0.036	0.082	0.026	0.073	0.054
A	0.037	0.000	0.013	0.056	0.027
Plot A Transition Matrix Elements					
P ₂	0.783	0.625	0.517	0.762	0.672
P ₃	0.900	0.900	0.846	0.750	0.849
P ₄	1.000	0.957	1.000	0.920	0.969
G ₁	0.042	0.017	0.007	0.003	0.017
G ₂	0.087	0.156	0.345	0.143	0.183
G ₃	0.100	0.100	0.154	0.200	0.138
Plot B Transition Matrix Elements					
P ₂	0.333	0.667	0.571	0.400	0.493
P ₃	0.750	0.460	0.857	0.857	0.731
P ₄	0.941	1.000	1.000	1.000	0.985
G ₁	0.003	0.005	0.001	0.002	0.003
G ₂	0.222	0.000	0.286	0.000	0.127
G ₃	0.188	0.460	0.143	0.143	0.234
Plot C Transition Matrix Elements					
P ₂	0.380	0.375	0.182	0.800	0.434
P ₃	0.700	0.500	0.667	0.571	0.610
P ₄	0.933	1.000	0.971	0.921	0.956
G ₁	0.014	0.010	0.002	0.003	0.007
G ₂	0.286	0.500	0.545	0.000	0.333
G ₃	0.267	0.385	0.278	0.286	0.304

mortality of the adult stage was positively but not significantly correlated with summer rainfall ($Y = 0.07X - 11.76$, $r = 0.90$, $P < 0.2$).

The number of flowers (all plots combined) and the number of fruits (all plots combined) were not significantly correlated with the amount of rainfall (for summer, winter or total) during the preceding year. The number of flowers ($Y = 49.97 + 0.44X$, $r = 0.72$) and the number of fruits ($Y = 60.86 + 0.46X$, $r = 0.68$) produced in all plots combined were weakly correlated with the amount of winter precipitation ($P < 0.2$ for both).

Growth and reproduction. Growth was determined as the change in plant diameter from one census to the next. There was a significant

TABLE 3. RAINFALL (mm) AT A SITE WITHIN 1.5 KM OF THE *CORYPHANTHA ROBBINSONUM* POPULATION IN COCHISE COUNTY, ARIZONA. Rainfall data are divided into summer (May through September) and winter (October through April of the following year). Means based on data from 1981 to 1992.

Year	Summer	Winter	Total
1988	367	168	535
1989	196	65	261
1990	155	199	354
1991	197	250	447
1992	229	227	456
1993	235	—	—
12 yr mean	260 ± 90	233 ± 127	493 ± 177

negative relationship between plant diameter and growth for three of the four between-year transitions (Table 4). Small plants increased in diameter at a greater rate than large plants. The negative relationships were not simply a result of using a linear dimension (plant diameter) to measure growth (which is three dimensional). For three of the years, half of the plants over 2 cm in diameter either did not grow or decreased in diameter (Table 5). After the 1992 census, 68% of the plants over 2 cm in diameter shrank or at least did not grow. Based on the linear regressions in Table 4, a plant was likely to shrink from one year to the next if its diameter exceeded 31.2 mm in 1990, 28.1 mm in 1991, and 20.0 mm in 1992. There was a modest, but not significant, correlation between the amount of winter precipitation occurring between two censuses (X; Table 3) and the slopes of the linear regressions (Y; Table 4) for the four between-year transitions ($Y = 0.47X - 14.81$, $r = 0.86$, $P = 0.1$) (r = correlation coefficient).

The percentage of *C. robbinsorum* plants that produced flowers and fruits increased with plant diameter (Fig. 3). The smallest plants that flowered (and fruited) were 13 mm in diameter. At 18 mm, over half of the plants both flowered and fruited. Of the plants ≥ 25 mm in diameter, over 94% flowered and 75% fruited. Large adults produced more flowers and fruits than did small adults (Fig. 4). Over

TABLE 4. LINEAR REGRESSIONS OF Y, CHANGE IN PLANT DIAMETER (cm) AFTER ONE YEAR ($t_0 + 1$), IN RELATION TO X, PLANT DIAMETER (cm) OF PRECEDING YEAR (t_0). $Y = a + bX$.

Year (t_0)	N	Slope (b)	Y-intercept (a)	P > F	X, when Y = 0
1989	142	-0.020	0.128	0.4275	6.35
1990	150	-0.076	0.239	0.0015	3.12
1991	155	-0.130	0.364	0.0001	2.81
1992	153	-0.063	0.128	0.0097	2.02

TABLE 5. NUMBER (AND PROPORTION) OF *CORYPHANTHA ROBBINSORUM* PLANTS GROWING OR NOT GROWING BETWEEN YEARS.

	Year (t_0)			
	1989	1990	1991	1992
Plants ≥ 2 cm				
Growing	24 (.53)	26 (.48)	33 (.53)	23 (.32)
Shrinking or not growing	21 (.47)	28 (.52)	29 (.47)	48 (.68)
Plants < 2 cm				
Growing	62 (.64)	67 (.70)	78 (.84)	38 (.46)
Shrinking or not growing	35 (.36)	29 (.30)	15 (.16)	44 (.54)
Total shrinking or not growing	56 (.39)	57 (.38)	44 (.28)	92 (.60)
Total	142	150	155	153

50% of all of the fruit produced during the five years by this population were from 25 individuals that represented only 23% of the adult population.

About 7.2% of the flowers did not set fruit. The flowers on small plants were more likely to set fruit than the flowers on large plants. When 4 categories of plant sizes (13–17, 18–22, 23–27 and 28–35 mm) were examined using a χ^2 test of homogeneity, the category of largest plants had a disproportionately greater frequency of flowers failing to set fruit ($\chi^2 = 11.2$, $0.025 < P < 0.01$) (Table 6). Plants with clusters of five or more flowers were also more likely to include flowers that did not set fruit when compared to plants with clusters of 1, 2, 3, or 4 flowers ($\chi^2 = 18.1$, $P < 0.001$) (Table 7).

Matrix analyses. The results of the matrix analyses are given in Table 8. For each plot, λ is greater than 1.0, indicating that the populations are growing. From the projection analysis, the population generation time, \bar{A} , is determined to be 16.9 years for Plot A, 60.7 years for Plot B and 17.3 years for Plot C.

The unrealistically large \bar{A} value calculated for Plot B must result from P_4 , G_1 , or G_2 , since these were the only parameters differing from their counterparts in Plots A and C. For Plot B, P_4 was greater

TABLE 6. THE NUMBER OF FLOWERS DEVELOPING INTO FRUITS IN RELATION TO PLANT DIAMETER. Data based on all years and all plots.

Number of flowers	Diameter of plant (cm)			
	1.3–1.7	1.8–2.2	2.3–2.7	2.8–3.5
Set fruit	46	217	205	189
Did not set fruit	2	11	12	26
Total	48	228	217	215

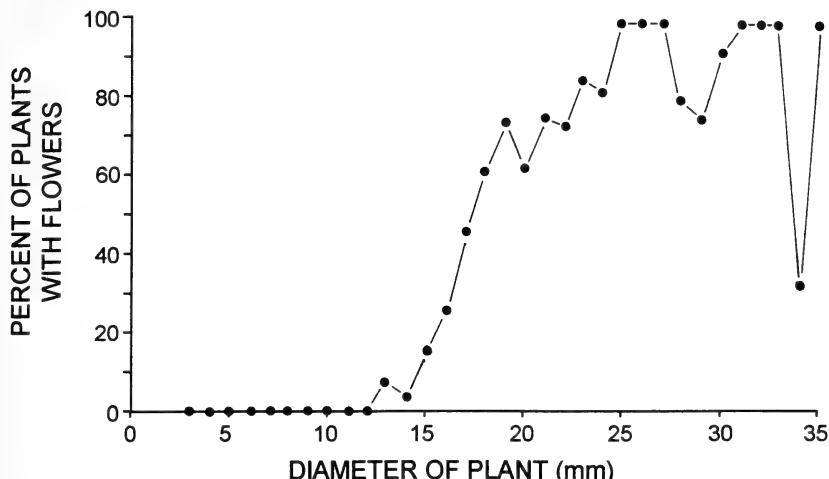


FIG. 3. Flower production by *C. robbinsorum* measured as the proportion of flower-bearing plants in 1 mm diameter increments. Data were collected in 1989–1993 from all plants within Plots A, B, and C. Data within each diameter class are pooled over five years.

while G_1 and G_2 were less than the same parameters for the other plots. When each of these parameters was adjusted so that it was within the range of values for Plots A and C, matrix analyses were performed changing a single parameter at a time. The effects of each of the three parameter changes on $\bar{\Lambda}$ (Table 9) suggests that the lower than usual values of G_2 and especially G_1 had the greatest effect on $\bar{\Lambda}$. Reducing the P_4 value of Plot B to one that was more like the other plots had only a modest effect on $\bar{\Lambda}$. When fecundity, F_4 , was increased to 80 or reduced to 9.6 and the matrices reanalyzed, there was no appreciable effect on either λ or $\bar{\Lambda}$ for any of the plots (Table 9).

For Plot C, the simulated 50% reduction in survivorship of each of the four stage-classes resulted in only a modest decrease in λ (but with λ still > 1) for seeds (to juveniles) (Table 9). Reducing the survivorship of J1 or J2 produced an intermediate effect on λ . If a stable age distribution could be (but can not be) obtained for the case of a 50% reduction in the survivorship of either J1 or J2, the predicted $\bar{\Lambda}$ values would be 451 years for J1's and 67,000 years for J2's. A 50% reduction in survival of the adult stage-class produced the greatest change in λ ; λ fell from +1 to 0.82.

For Plot C, simulations were made of the effect of increasing survivorship for each stage-class (Table 9). A modest increase in λ is seen when seed bank survival (P_1) is increased from 0 to 0.5. A profound increase in λ is noted when any other P value is raised to 1.0.

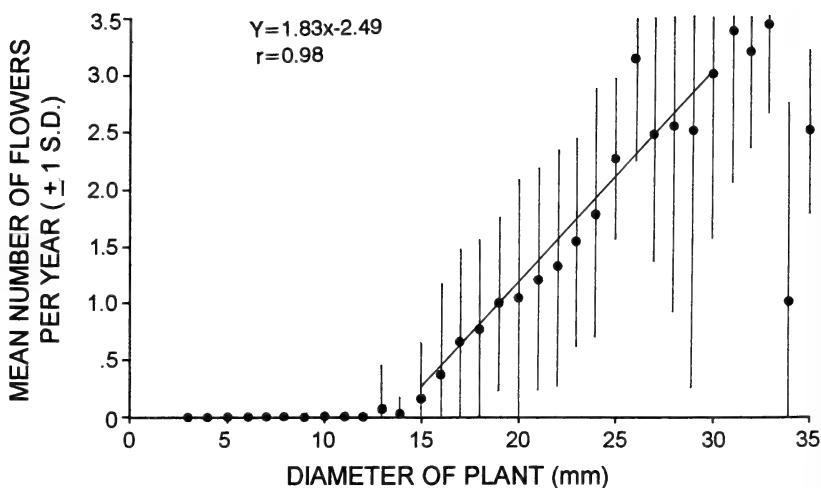
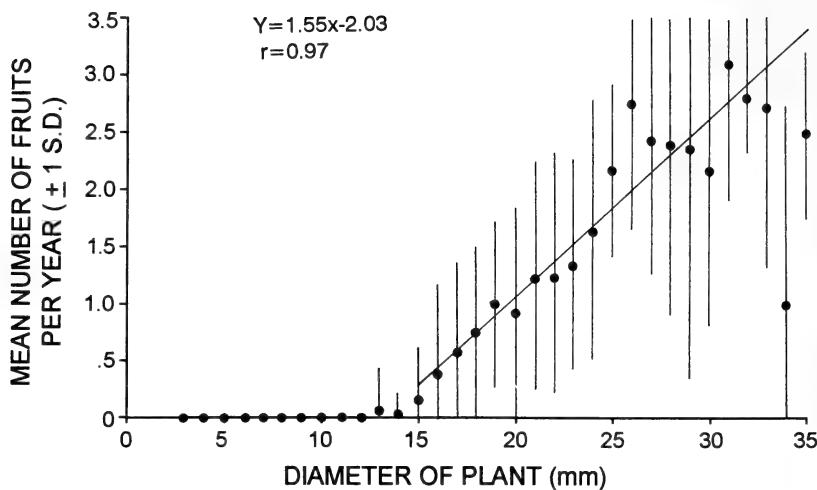


FIG. 4. Relationship between plant diameter and number of flowers and fruits produced by individuals of *C. robbinsorum*, Cochise County, Arizona. Mean production of flowers and fruits based on all individuals (regardless of their stage) in each size class. Vertical bars = one standard deviation.

TABLE 7. THE NUMBER OF PLANTS WITH ALL FLOWERS PRODUCED IN A YEAR SETTING FRUIT OR ONE OR MORE OF THE FLOWERS NOT SETTING FRUIT. Data based on all years and all plots.

Number of plants	Number of flowers produced per season				
	1	2	3	4	5-7
All flowers set	119	102	55	18	6
1 or more flowers not set	9	12	6	7	4

DISCUSSION

Effect of rainfall on demographic parameters. *Coryphantha robbinsorum* had several unanticipated responses to rainfall regimes. Increased rainfall was expected to increase survivorship, especially for the smallest size-class. However, the only stage-class that appeared to benefit from increased rain was J1; J1 survivorship increased with increasing winter rainfall. Previous studies of cacti have shown that survival of the youngest stage-classes increases with increased rainfall (Johnson et al. 1993; Steenbergh and Lowe 1969). Increased annual rainfall appeared to decrease the number of new J1's to the population. There also appeared to be a modest increase in the mortality of adults after summers with more rainfall.

Although the causes of mortality of *C. robbinsorum* were not determined in this study, several factors should be considered. The plants occur in the cracks of limestone outcrops, in well-drained microsites (U.S. Fish and Wildlife Service 1993). Another cactus, *Carnegiea gigantea*, is restricted to natural rock piles in the southern portion of its range (Steenbergh and Lowe 1977, p. 118). The rock piles are thought to afford well-drained sites in an area (extreme southern Sonora, Mexico) that often has saturated soils after hot summer rains. Hot humid conditions increase the susceptibility of cactus plants to lethal infestations of fungi (Booth and Alcorn 1959; Gene Joseph personal communication 1993). In the same context, four cacti that occur on gravel or well-drained limestone outcrops in southern Arizona, *C. robbinsorum*, *Echinocereus fendleri*, *E. pectinatus* var. *rigidissimus*, and *Neolloydia intertexta*, when grown

TABLE 8. THE RESULTS OF MATRIX ANALYSIS OF DEMOGRAPHIC DATA FROM THREE *C. ROBBINSORUM* MONITORING PLOTS. Data pooled for all years for each plot. Ages are expressed in years.

λ	Mean age as seed	Mean age as J1	Mean age as J2	Mean age as adult	Population generation time
Plot A	1.094	1.000	2.031	4.425	9.343
Plot B	1.003	1.000	1.378	3.431	53.655
Plot C	1.041	1.000	1.107	5.125	17.301

TABLE 9. SENSITIVITY ANALYSIS OF *C. ROBBINSORUM* POPULATIONS. Resultant λ and \bar{A} , 'baseline runs' and after (1) simulated adjustment of three parameters for the matrix of Plot B so that these parameters resemble the same parameters of Plots A and C, (2) simulated change in fecundity from a baseline of 33 seeds per plant per year to 80 seeds and to 9.6 seeds (3) simulated 50% decrease in survival probabilities of parameters for Plot C, and (4) simulated increase in survival probabilities of parameters for Plot C.

Stage parameter	Change in initial matrix		Result	
	Old	New	λ	\bar{A}
Adjustment of Plot B Parameters				
	baseline run		1.003	60.695
P_4	.985	9.60	.982	52.413
G_1	.003	.010	1.041	25.009
G_2	.127	.250	1.018	37.124
Change in Fecundity				
Plot A				
$F_4 = 33$.017	—	1.094	16.799
$F_4 = 80$.017	.006	1.083	17.741
$F_4 = 9.6$.017	.037	1.067	19.546
Plot B				
$F_4 = 33$.003	—	1.004	60.695
$F_4 = 80$.003	.001	1.004	60.398
$F_4 = 9.6$.003	.009	1.003	61.539
Plot C				
$F_4 = 33$.007	—	1.042	17.301
$F_4 = 80$.007	.003	1.041	17.351
$F_4 = 9.6$.007	.023	1.0378	17.825
50% Decrease in Plot C Parameters				
	baseline run		1.041	17.301
G_1	.007	.004	1.007	25.042
P_2	.434	.204	.958	451.420
G_2	.333	.008		
P_3	.609	.303	.956	67,487.000
G_3	.304	<.001		
P_4	.956	.478	.822	9.371
Increase in Plot C Parameters				
P_1	.000	.500	1.085	14.209
P_1	.000	1.000	12.048	14.312
P_2	.434	1.000	11.685	15.525
P_3	.609	1.000	11.483	16.324
P_4	.956	1.000	10.734	19.610

commercially are more likely to die than other cactus species after rains or irrigation during late summer and early fall (Gene Joseph personal communication 1993).

Coryphantha robbinsorum flower buds develop on the previous year's growth (Hildegard Nase personal communication 1993). Although reproductive output responds to increased rainfall for other

cacti (Johnson et al. 1993; Steenbergh and Lowe 1983), there was only a weak correlation between amount of winter rainfall and number of flowers and fruits produced by the entire study population.

Growth and reproduction. There are two unusual features of *Coryphantha robbinsorum* growth. The first is that, while most juveniles increased in diameter from year to year, about half of the adults over 2 cm in diameter either did not change or decreased in diameter between years. The other feature is that there was a greater tendency of plants to shrink from one year to the next with wetter intervening winters. *Coryphantha robbinsorum* in the wild may be as susceptible to root rot in winter as cultivated populations of cacti.

Plants did not begin to reproduce until they were at least 13 mm in diameter. The relationship between increasing plant size and the probability of flowering for *C. robbinsorum* resembles that of *Echinomastus erectocentrus* var. *acunensis* (Johnson et al. 1993). Large adults (≥ 25 mm diameter) were more likely to flower than small adults and, because they also were more likely to have more flowers and fruits per individual than small individuals, contributed a disproportionate number of fruit to the population.

Steenbergh and Lowe (1977) demonstrated experimentally that 50% of the potential stem growth per year of small (4–5 m height) *Carnegiea gigantea* individuals is diverted into its yearly reproductive effort. If the reproductive investment were similar for small *C. robbinsorum*, small adult plants might be more resource-limited than large adults during reproductive bouts and more likely to respond to this limitation by aborting ripening fruit more frequently than adults. Flowers produced by the largest adults (2.8–3.5 mm) were more likely to abort than flowers produced by any other flowering size-class. Plants with large flower clusters (≥ 5 flowers per plant) were more likely to include flowers that failed to set fruit than plants with single flowers or smaller clusters. A single flower of *C. robbinsorum* reopens each day for about seven days (Hildegard Nase personal communication 1993). We do not know if the number of flowers per cluster affects pollinator movement nor what other factors may be responsible for the reduced fruit set of larger adults.

Matrix analysis. Several important attributes of the population and of the characteristic life history of *Coryphantha robbinsorum* become available with matrix analysis. One attribute of the population, λ , is greater than 1.0 for each of the plots. A λ greater than 1.0 indicates that the population is currently expanding in each of these plots. The mean λ for the three plots, 1.0464, predicts a doubling time for the population of about 16 years. The λ values of the three plots are very similar. Comparison with other published values of λ (Burns and Ogden 1985; Pinero et al. 1984; Caswell 1986)

suggests that *C. robbinsorum* has a finite rate of population increase more similar to that measured for the large understory palm, *Astrocaryum*, and both tropical and temperate tree species than that measured for most herbaceous plants.

The behavior of the populations of small dense patches of *C. robbinsorum* needs to be examined over a longer time period. Since the known populations of this cactus are nowhere both dense and extensive, the measured value of λ is expected to decrease over time in these study plots. When λ decreases, appropriate monitoring of the populations may detect if density-dependent mortality factors are regulating population size.

Zimmerman (1985 and personal communication 1993) has hypothesized that predation (or parasitism) may be one factor regulating the densities and distribution patterns of *Coryphantha robbinsorum* populations. Zimmerman has found *C. robbinsorum* plants freshly killed by a cerambycid beetle (*Moneilema corrugans*), a cactus weevil (*Gerstaeckeria* sp.) and a *Yosemitia* sp. moth. The larvae of these insects feed on the internal tissues and can kill adult plants, particularly by damaging the xylem. However, the causes of mortality in relation to population density remain unexplored for *C. robbinsorum*.

Sensitivity and elasticity analyses performed on these matrices demonstrated that the value of λ in these three plots was largely dependent on the survival (P_4) of the adult population. Altering fecundity or seedling establishment has little effect on λ in these three plots. Management schemes to safeguard populations of *C. robbinsorum* should focus on protection of adult plants. A management scheme that focuses on adult plants would be similar to that recommended by Crouse et al. (1987) for the Atlantic populations of loggerhead sea turtles (*Caretta caretta*). P_i and G_i values of the late juveniles and adults for both populations have the greatest effect on λ .

This study is the first one to estimate the population generation time, \bar{A} (=mean age of parents contributing seed to the next generation at a stable age distribution), of any cactus. The value of \bar{A} obtained for Plots A and C suggest that the average adult age in situ is about 17 years. However, most species of small cacti appear to reach adulthood much sooner in horticulture than in situ. With the enhanced growing conditions in cultivation, some individuals of *C. robbinsorum* flower in their second year and most in their third year (Gene Joseph personal communication 1993; Hildegard Nase personal communication 1993). One small cactus that requires a long time to mature in cultivation is *Echinocactus horizonthalonius* var. *nicholi*. Mark Dimmitt (personal communication 1993) has found that this plant requires at least 10 years to flower from seed in

cultivation and estimates that individuals in nature may require at least 30 years to mature.

ACKNOWLEDGMENTS

For invaluable assistance in performing the plant monitoring, we thank Kevin Cobble, Mark Cochran, Dave Gori, Kristen Johnson, Jeff Krausmann, and Peter Warren. Gene Joseph, Hildegard Nase, Mark Dimmitt and Allan Zimmerman generously shared their wealth of experience with cacti. Gordon Fox helped greatly in the manipulation of the STAGECOACH program and interpretation of results. Diane Wheeler freely gave of her time in the growth analyses. Funding for the demographic analysis was provided by the U.S. Fish and Wildlife Service (Purchase Order 20181-2-1089).

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(Received 4 Feb 1994; accepted 29 Nov 1994)

ANNOUNCEMENT

THE RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Ing. Nelson Zamora, of the Instituto Nacional de Biodiversidad (INBio), Costa Rica, is the recipient of the **1994 Rupert Barneby Award**. Ing. Zamora will be working on several groups of Mimosoid and Caesalpinioideae Legumes for Costa Rica.

The New York Botanical Garden also invites applications for the **1995 Rupert Barneby Award**. The award of \$1,000.00 is to assist researchers planning to come to The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought, and how the collection at NYBG will benefit their research. Travel to NYBG should be planned between January 1, 1996 and January 31, 1997. The letter should be addressed to Dr. Enrique Forero, Director, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126 USA, and received no later than December 1, 1995. Announcement of the recipient will be made by December 15th. Anyone interested in making a contribution to **THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS**, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Forero.

COMPARISON OF THE INFLUENCE OF TWO EXOTIC COMMUNITIES ON ECOSYSTEM PROCESSES IN THE BERKELEY HILLS

MARCOS ROBLES^{1,2}

Environmental Science, University of California
Berkeley, CA 94720

F. S. CHAPIN, III

Department of Integrative Biology, University of California
Berkeley, CA 94720

ABSTRACT

The introduction of exotic plant species can provide insight into the biotic regulation of ecosystem processes. Many coastal California ecosystems have been changed by the introduction of exotic species, two of which are the blue-gum eucalyptus species (*Eucalyptus globulus*) and annual grasses species in the genera *Bromus*, *Avena* and *Lolium*. In this study, we compared the rates of ecosystem processes such as production and decomposition on sites dominated by these two exotic communities. *Eucalyptus* litter was produced in greater quantity and decomposed more slowly than litter produced in annual grasslands. Consequently, the litter layer in *Eucalyptus* sites was nine times larger than in annual grasslands. These results indicate that, under similar climatic and edaphic conditions, the characteristics of the plant species caused large differences in ecosystem processes.

State factors governing ecosystem processes include climate, parent material, topography, time, and biota (Jenny 1941, 1980). Of these factors, the influence of the biota has received the least attention. The invasion of exotic species provides an opportunity to study the impact of plant species on rates of ecosystem processes such as productivity and nutrient cycling (Vitousek 1990). For example, nitrogen-fixing exotic species can alter nutrient cycling (Vitousek et al. 1987), while other exotic species can alter disturbance regimes (D'Antonio and Vitousek 1992).

It is usually difficult to study biotic effects on ecosystem processes because different communities occupy different positions along environmental gradients. Coastal California provides a unique opportunity to study biotic effects on ecosystem processes because of a wide range of introduced species. Annual grasslands and *Eucalyptus* groves, both widespread exotic communities in California, have very different life-histories and phenologies which may influ-

¹ Current Address: Graduate Degree Program in Ecology, Colorado State University Ft. Collins, CO 80523

² Reprint requests may be sent to Robin Kelly, Natural Resources Ecology Laboratory, Colorado State University, Ft. Collins, CO 80523.

ence ecosystem processes. *Eucalyptus globulus* is a long-lived, evergreen tree which is active throughout the year, whereas annual grasses in the genera *Bromus*, *Avena*, and *Lolium* are annuals which are active only for a small portion of the year (Heady 1977).

The purpose of this study was to determine whether or not these exotic communities exhibit different rates of litter production and decomposition, and if so, to determine to what extent these differences may be attributed to the life form characteristics of the dominant plants. We expected that *Eucalyptus* groves would exhibit larger litter layers than annual grasslands because (1) on an annual basis, *Eucalyptus* trees produce more litter than annual grasses and (2) *Eucalyptus* litter decomposes slower than grass litter.

STUDY SITE AND METHODS

The study was conducted in Tilden Park near Berkeley, California (Fig. 1). The long-term averages of precipitation and temperature at the site are 47.5 cm and 14.1°C, respectively (WRCC 1993). In 1992–1993, when the study was conducted, annual precipitation was 67.6 cm and mean temperature was 15.9°C (WRCC 1993). Five paired sites of *Eucalyptus* groves and annual grasslands were selected, each of at least 400 m² area and between 700–800 ft elevation (Fig. 1). All sites were on west-facing slopes. Two sites were located on soils derived from volcanic parent material, whereas the other three sites were on soils derived from a sandstone conglomerate material (Gordon personal communication).

Aboveground litter production of annual grasses was estimated by weighing standing live biomass inside two 20 cm × 20 cm quadrats placed at random points along a 20 m transect. In all cases, random points along the transect were determined using a random numbers table. Aboveground biomass was clipped at the ground surface at the end of the growing season (mid July 1992) and pooled for the two quadrats. Current year's aboveground biomass was separated, oven-dried for 24 hours at 55°C and weighed.

Aboveground *Eucalyptus* litter production was estimated by weighing recent litter (i.e., leaves, stems, bark, fruit) that fell into two 50 cm × 50 cm litter traps placed at random points along a 20 m transect at each site. At the end of each month, the two samples from each site were pooled, oven-dried for 24 hours at 55°C, and weighed. Litter was collected twice in 1993, at the end of February and May, for a total of 11 months of litter production data.

In each forest and grassland site, the litter layer was sampled in five 20 cm × 20 cm quadrats placed at random points along a 20 m transect. *Eucalyptus* litter was divided into two layers, fresh and duff. Fresh litter included all green or light-brown *Eucalyptus* leaves, stems and bark that were only partially decomposed, whereas the

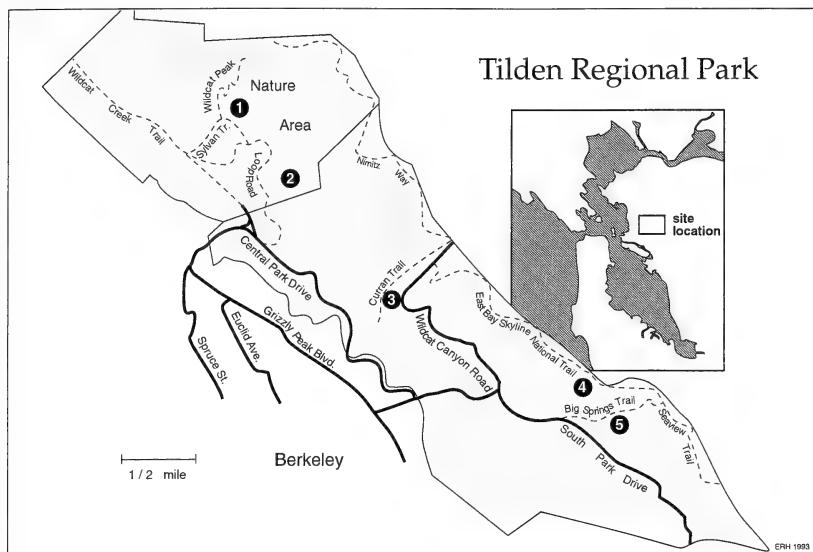


FIG. 1. Map of Tilden Regional Park. Sites 1–5 are indicated by the circled numbers.
Source: After EBRPD, 1992. Cartography by Eric R. Havel.

duff layer consisted of more highly decomposed material. There was no duff layer in the grassland. In both cases, litter was collected down to the mineral soil.

To estimate decomposition, 100 grams of fresh litter were collected from one *Eucalyptus* and one grassland site. We estimated the *Eucalyptus* litter to be less than one month old (based on observations of one-month-old litter collected in the litter traps). After removing the dark brown stems from the grass litter, it was assumed that the remaining golden-brown litter was the current year's biomass. Fifteen gram subsamples of each litter type were air dried, and 5 grams were placed in 20 cm × 20 cm nylon mesh bags. Of the other 10 grams in each sample, five grams were oven-dried at 55°C for 24 hours. The dried samples were weighed to determine the actual oven-dry weight of the initial litter. The remaining five grams were used to determine total carbon and nitrogen present in the initial litter. Four litter bags of each litter type were randomly placed along a 20 m transect on each of the 10 sites in early November. In mid-February (after 86 days of decomposition) and late April (after 172 days), two *Eucalyptus* and two annual grass bags from each site were collected. These samples were oven-dried at 55°C for 24 hours, weighed, ground and analyzed for total carbon and nitrogen using a Carbo Erba 1500 C/N analyzer.

All statistical analyses were performed using 2-way ANOVAs in

Systat (Systat 1990). The two independent factors, species and site, and interactions between these two were tested for significance ($P < 0.05$).

RESULTS

Aboveground litter production of *Eucalyptus globulus* stands during the initial six months was 295 g/m² (Table 1). There was no consistent pattern of litter production during these six months. In the last five months (Jan–May 1993), the litter mass was 202 g/m² for an 11 month total of 497 g/m². This amount is more than twice the annual aboveground litter production of grasses, 184 g/m² (Table 1). *Eucalyptus* litter layers contained 9 times more material (6.00 kg/m²) than the annual grasses (0.69 kg/m²) (Table 1). The *Eucalyptus* litter layer was dominated by the duff layer.

After 86 days of decomposition in the field, mass loss did not differ between species or site (Fig. 2a). However, *Eucalyptus* litter lost N, whereas grass litter gained N (Fig. 3), so that after 86 days, the C/N ratio of *Eucalyptus* litter was significantly higher than that of annual grass litter (Fig. 2b). After 172 days of decomposition, annual grass litter had lost a significantly greater proportion of its initial mass (Fig. 2a) and nitrogen (Fig. 3) than did the *Eucalyptus* litter. *Eucalyptus* litter in the *Eucalyptus* site decomposed faster than *Eucalyptus* litter transplanted into the grassland (Fig. 2a). The C/N ratios of this period were consistent with the mass loss results. The grass C/N, after 172 days, was significantly lower than the *Eucalyptus* C/N, and the C/N of the *Eucalyptus* litter placed on *Eucalyptus* sites was significantly lower than on grass sites (Fig. 2b).

DISCUSSION

The estimate of *Eucalyptus* litter production in this study (497 g/m²) is lower than other studies of *Eucalyptus* species in wetter environments (700–900 g/m², Binkley et al. 1992; 1500 g/m², Lugo et al. 1990). The grass litter production reported here (184 g/m²) is within the range, (78–290 g/m²) of long-term litter production of annual grasses (Heady 1977). Even though the *Eucalyptus* litter production estimate is low, it is over two times larger than the grass litter production. Because these two communities were under similar climatic and edaphic conditions, this result, as well as the large difference in litter layer mass, suggest that the inherent characteristics of the community dominants may explain differences in litter production. *Eucalyptus* trees contain leaves which are active 12 months of a year, whereas annual grass leaves are active for only 7–8 months of the year (Heady 1977).

TABLE 1. LITTER PRODUCTION AND LITTER LAYER MASSES PRESENT ON *EUCALYPTUS* AND ANNUAL GRASS SITES. Numbers are means of replicate samples ($n = 10$) and standard errors. Estimates of litter production between Jan–Feb and Mar–May were increased by 10% to account for decomposition in the field (Fig. 2a). Total for *Eucalyptus* litter production and fuel load were significantly larger than those of annual grasses.

Month	<i>Eucalyptus</i> litter production (g/m ²)	Annual grass litter production (g/m ²)	<i>Eucalyptus</i> fuel load (kg/m ²)	Annual grass fuel load (kg/m ²)
July	38 ± 2		duff 5.4 ± 0.5	
August	25 ± 3		fresh 0.6 ± 0.06	0.69 ± 0.05
September	60 ± 8			
October	49 ± 5			
November	35 ± 7			
December	88 ± 9			
Jan–Feb	103 ± 24			
Mar–May	99 ± 15			
Total	497 ± 41	184 ± 25	6.0 ± 0.58	0.69 ± 0.05

As with litter production, litter decomposition was governed by inherent differences between the species, in this case the quality of litter. Because the litter of many *Eucalyptus* species contains large amounts of lignin and resin (O'Connell 1988), we suspect the high initial carbon concentration in the *Eucalyptus* litter (data not shown) resulted from substantial amounts of lignin relative to the grass tissue. Thus, the slower decomposition of *Eucalyptus* litter on both sites seen after 184 days can be explained by the life-form difference.

The results of the second decomposition period showed that *Eucalyptus* litter was prone to decompose faster in the *Eucalyptus* sites than in annual grass sites. Microbes in the *Eucalyptus* groves may be better suited (via natural selection) to consume *Eucalyptus* litter than microbes in the annual grasslands. If so, litter type has a secondary, indirect influence on decomposition via specialization of microbial fauna.

The N dynamics of decaying leaf litter provide insight into feedbacks between species and ecosystem processes. After 86 days of decomposition, *Eucalyptus* litter lost N while annual grass litter immobilized N (Fig. 3). The decreasing N content in *Eucalyptus* litter may have led to higher soil N mineralization rates during this period (McClaugerty et al. 1985). This trend was reversed during the second decomposition interval, where more N was lost in the grass sites than in the *Eucalyptus* sites (Fig. 3). Because the quality of *Eucalyptus* litter after this interval was low compared to the grass litter, we expected the trend of N retention in the *Eucalyptus* litter relative to grass litter to continue and act as a negative feedback

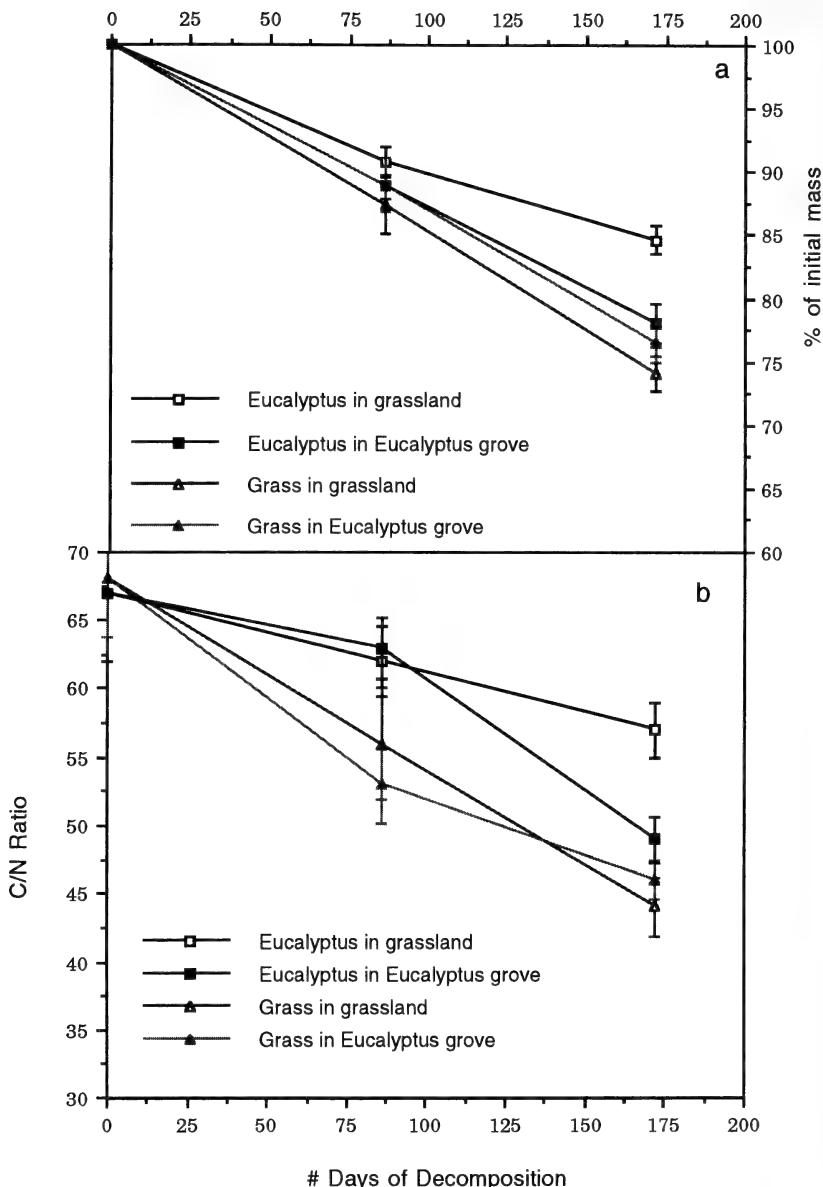


FIG. 2. (a) Percent of initial biomass of litter types placed on *Eucalyptus* and annual grass sites calculated as: $(\text{Initial Mass} - \text{Final Mass})/\text{Initial Mass} \cdot 100$. Differences between litter types and between *Eucalyptus* litter on each site were significant at 172 days. Vertical bars in (a) and (b) represent standard errors. (b) C:N ratios of litter types placed on *Eucalyptus* and annual grass sites. Differences between litter types were significant at 86 and 172 days and differences between native and transplanted *Eucalyptus* litter were significant at 172 days.

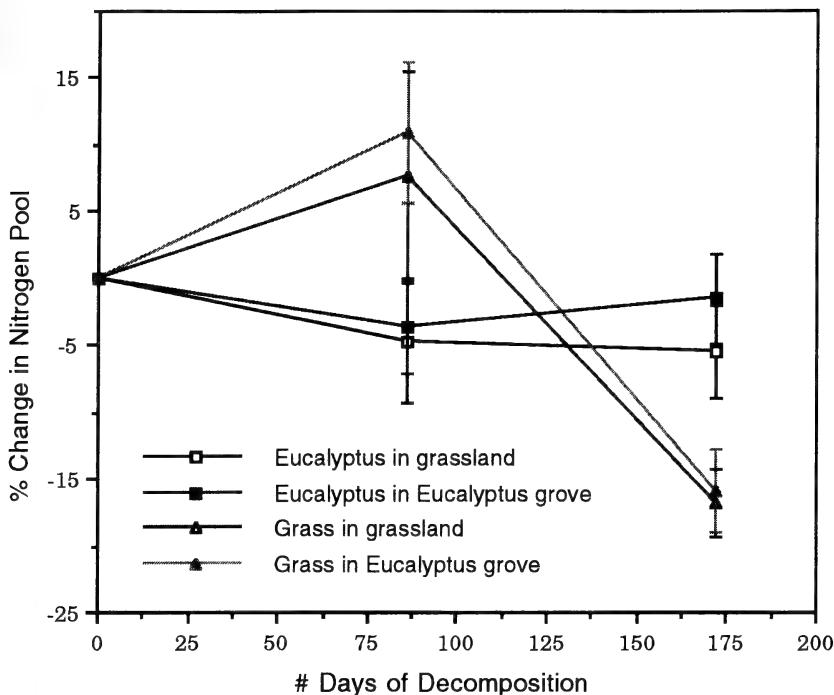


FIG. 3. Percent change in N pool of litter types on both sites calculated as: (grams N of initial litter – grams N final litter)/(grams N of initial litter).

between litter production and N availability. *Eucalyptus* trees may be able to sustain high litter production rates despite slow rates of decomposition and soil N mineralization by exploring deeper layers in the soil profile. The root profiles of *Eucalyptus* trees are much more extensive at deeper depths than those of annual grasses which are typically concentrated in the top 5–10 cm (Jackson et al. 1988). Thus, stands of *Eucalyptus* are sustained by a difference in life-form (i.e., rooting depth) once they establish and alter the N cycling of the site.

One important consequence of exotic species invasions is the alteration of disturbance regimes (Vitousek 1990; D'Antonio and Vitousek 1992). The East Bay fire of October 1991 is a recent example of the many wildfires that plague the coastal hills of California. What role did *Eucalyptus* groves and annual grasslands play in this and other fires? Using computer simulation, Van Wilgen and Richardson (1985) found that exotic shrubs that produced larger litter layers than native shrubs exhibited lower simulated rates of fire spread and intensity due to densely-packed litter layers. They concluded that

densely packed litter layers may increase fire hazard only under extreme conditions, such as very dry conditions. These results may apply to this system, in that one community, *Eucalyptus* groves, produced large amounts of densely-packed litter, whereas another, annual grasslands, produced small amounts of litter which is less densely-packed. One consequence of this apparent pattern is that *Eucalyptus* may influence fire intensity whereas annual grasses may influence fire frequency in the California coastal hills.

ACKNOWLEDGMENTS

This research would not have been possible without the permission to study Tilden Park given by Ron Russo and East Bay Regional Parks District (EBRPD). We thank D. Sloan, K. Taylor, M. A. Vinton, R. H. Kelly and I. C. Burke for providing insight into the focus of this project, for offering suggestions of field design and data analysis, and for the critical review of this paper.

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(Received 10 Sept 1993; accepted 20 Jan 1995)

ANNOUNCEMENT

CALIFORNIA EXOTIC PEST PLANT SYMPOSIUM 1995

October 6-8, 1995

Asilomar Conference Center, Pacific Grove California

The California Exotic Pest Plant Council (CalEPPC) announces the fourth annual symposium dealing with a major environmental threat recently attracting nationwide attention. This is the threat to California's natural ecosystems by invasive non-native plant species introduced from around the world.

In California, and throughout the nation, exotic pest plants pose the greatest single threat to the long term integrity of many natural areas and ecosystems. According to one estimate prepared by the Bureau of Land Management, infestations of exotic pest plants are increasing at the rate of approximately 4600 acres per day on disturbed and undisturbed public lands of the west.

The symposium will bring together experts, land managers, public and non-profit agency staff, field practitioners, and concerned citizens who are developing solutions to this major ecological problem. A prominent theme of this year's symposium will be biocontrol—the intentional introduction of carefully selected predator species to control invasive plants.

The keynote speaker will be Randy Westbrooks who will speak on the current weaknesses of APHIS, and how it could be revamped to do a better job. The program and poster sessions will include presentations on the biology of non-native plant invasions, perspectives on biocontrol, and examples of successful control efforts in California and Australia. There will be ample opportunity for participants to exchange ideas and to become involved in CalEPPC projects and programs. A field trip to local habitat restoration sites will cap the symposium on Sunday morning.

For further information contact Sally Davis, P.O. Box 1045, Cambria, CA 93428-1045. Telephone (805) 927-7187.

THE VEGETATION AND FLORA OF THE MARIN ISLANDS, CALIFORNIA

ROBERT ORNDUFF

Department of Integrative Biology, University of California,
Berkeley, CA 94720-3140

MICHAEL C. VASEY

Department of Biology, San Francisco State University,
San Francisco, CA 94132

ABSTRACT

The Marin Islands in San Francisco Bay are two very small islands a short distance off the shore of San Rafael, Marin County, California. The vegetation and floras of the two islands are strikingly different. The herbaceous flora of the plateau on West Marin Island is dominated by a dense sward of the introduced annual grasses *Bromus diandrus* and *Avena fatua*, whereas the flora of the plateau on East Marin Island is dominated by a mixture of smaller, introduced grass species growing with several perennial and annual native forbs and grasses. Snowy Egrets, Great Egrets, Black-crowned Night Herons, Great Blue Herons, Western Gulls, and Canada Geese nest on West Marin Island; of these, only Canada Geese nest sparingly on East Marin Island. We attribute the floristic and vegetational differences between these islands to alterations of soil chemistry by bird guano and physical disturbances of the vegetation caused by the birds on West Marin Island, factors that are largely missing from East Marin Island, which was, until very recently, inhabited. The vegetation of both islands includes mixed evergreen forest, coastal prairie, coastal salt marsh, and northern coastal scrub. Several species of introduced ornamental trees, shrubs, and herbs grow on East Marin Island but not on West Marin Island. Both islands support a partially fringing woodland of *Quercus agrifolia*, *Aesculus californica*, and *Umbellularia californica*. The native *Sanicula crassicaulis*, *Stachys ajugoides* var. *rigida*, *Dryopteris arguta*, *Lonicera hispidula* var. *vacillans*, and *Symporicarpus albus* var. *laevigatus* were frequent on East Marin Island but were not observed on West Marin Island; *Claytonia perfoliata* and *Polypodium californicum* were abundant on the former island but were sparingly represented on the latter one. The known native vascular flora of the two islands consists of 65 species; 26 of these occur on both islands, 37 are known only from East Marin Island, and two were collected only on West Marin Island.

The Marin Islands occur in San Rafael Bay, an arm of San Francisco Bay, approximately midway between Point San Pedro and Point San Quentin, Marin County, and ca. 0.8 km south of the nearest mainland point at San Rafael. West Marin Island is more or less ovate in outline, ca. 0.2 km long, and ca. 1.1 ha in area; East Marin Island is roughly L-shaped, ca. 0.4 km long, and ca. 4.2 ha in area. The two islands are separated from each other by ca. 170 m of water. All sides of each island are marked by steep cliffs, but the tops of the islands are more or less flat; the maximum elevation

of the islands is ca. 20 m. In 1992, these islands came under the management of the U.S. Fish and Wildlife Service as The Marin Islands National Wildlife Refuge and State Ecological Preserve (Greene 1993). West Marin Island is a very important breeding site for Snowy Egrets, Great Egrets, Black-crowned Night Herons, and Great Blue Herons, all of which nest in the trees, and Western Gulls and Canada Geese, which nest on the ground. However, possibly because of prolonged human occupancy of East Marin Island, in 1993 the only birds of the foregoing group we observed nesting on East Marin Island were a few pairs of Canada Geese.

We were invited to undertake a floristic survey of the native plants of the Marin Islands by Richard Spight, a prime mover in negotiating their transfer from private to public ownership. The senior author or both authors visited these islands to observe and collect plants in October, 1991, and on 23 January and 16 March, 1992. The senior author made additional collections on East Marin Island on 2 June 1993. Because access to both islands was limited by the tides, we took only diagnostic fragments of the plants present and did not prepare voucher specimens. The only other botanical survey of the islands of which we are aware is that of Kroll (1991) who described the native and introduced vegetation of East Marin Island.

The natural vegetation of the Marin Islands consists of mixed evergreen forest, coastal prairie, coastal salt marsh, and northern coastal scrub (as recognized by Munz and Keck in Munz 1973). Howell (1970) circumscribed plant communities in Marin County somewhat differently; in his scheme, the natural vegetation of the Marin Islands consists of oak-buckeye forest (seven of the ten "more common" woody species he listed for this community grow together on East Marin Island), coastal brush, hill and valley grassland, and salt marsh. A recent account of Marin County plant communities (Shuford and Timossi 1989) mostly utilized the community names of Munz and Keck, but recognized associations within these. According to these authors, the forest association on the Marin Islands is oak-bay-madrone (but with madrone missing) and the scrub association is coastal sage-coyote brush scrub. Coastal prairie and coastal salt marsh were also recognized by these authors. Because the vegetation and flora of the two islands are different, these features will be described separately for each island.

EAST MARIN ISLAND

The plateau region of East Marin Island is dominated by several species of introduced trees, the most common of which is *Pinus radiata*. Several of the non-native plant species on the island were introduced as ornamentals, and some of these have become naturalized on the island. In addition, a number of introduced "weeds"

are also present on the island, probably as a result of accidental introductions. Elizabeth McClintock, who joined us on some of our visits, has recorded 46 introduced species of angiosperms on this island (McClintock personal communication).

A small herd of Barbary sheep (*Ammotragus lervia*) was introduced to this island in the 1980's to reduce vegetative cover and hence fire risk; in 1991, the sheep were removed. Their impact on the flora is unknown. In 1992, a resident caretaker left the island, leaving it uninhabited.

The natural forest on East Marin Island consists of *Quercus agrifolia*, *Aesculus californica*, and *Umbellularia californica*. These trees are common and occur mostly on the sheltered, moister northern side of the island. The understory consists of a few shrub species such as *Toxicodendron diversilobum* (which, however, occurs elsewhere on the island), *Symphoricarpos albus* var. *laevigatus*, *Holodiscus discolor*, *Rosa gymnocarpa*, and *Sambucus mexicana*. A common shrub along the edge of this forest is *Heteromeles arbutifolia*, which occurs elsewhere on the island as well. *Lonicera hispidula* var. *vacillans* is a common woody vine climbing in the trees. The herbaceous understory includes three ferns: *Dryopteris arguta* and *Polypodium californicum*, both of which are common, and *Adiantum jordanii*, which is uncommon. Of the native herbaceous angiosperms, only *Scrophularia californica* appears to be limited to this forest community. Other herbaceous species may occur both in this community and elsewhere on the island.

Northern coastal scrub is well developed on East Marin Island, occurring at the tops and faces of the cliffs along the western, southern, and eastern portions of the island. *Artemisia californica*, *Eriophyllum staechadifolium*, and *Mimulus aurantiacus* are common components of this community. We noted only a single individual of *Baccharis pilularis* on the island in 1991–1993. During that time there were numerous, apparently drought-killed shrubs in the scrub on this island, which appeared to be mostly if not exclusively introduced brooms (*Cytisus* or *Genista* spp.).

Despite the density of several introduced trees on East Marin Island, notably concentrated on the plateau, the prairie community that presumably predates the introduction of these trees still persists, although the species richness may have decreased due to shading and competition from the exotics. The native perennial grass *Nassella lepida* is abundant on the plateau. Common native forbs that occur with this grass include *Chlorogalum pomeridianum*, *Sanicula crassicaulis*, and *Stachys ajugoides* var. *rigida*. Other forbs that occur in the grassland, but elsewhere on the island as well, are *Eschscholzia californica* and *Claytonia perfoliata*, both of which are common, and scattered plants of *Gnaphalium stramineum* and *Achillea millefolium*. *Carex barbara* forms large, conspicuous swards in a few places.

Dichondra donelliana occurs locally on the eastern end of the island, but may have been introduced to the site. Kroll (1991) believed that the *Rubus* on the island is native, but we consider it to be the introduced *R. discolor* Weihe & Nees as does McClintock (personal communication).

A small pond of artificial origin occurs at the base of a quarried cliff on the south side of East Marin Island. The pond margin is occupied by a very depauperate coastal salt marsh, with *Distichlis spicata*, also noted as scattered individuals on the rocky south shore, *Jaumea carnosa*, and *Salicornia virginica* present. The aquatic green alga *Cladophora* sp. and *Ruppia maritima* are present in this pond.

Several plant species, many of which are common on the island, do not occur in well-defined, generally recognized plant communities. For example, *Dudleya cymosa* ssp. *paniculata*, *Eriogonum nudum*, *Lotus scoparius*, and *Spergularia macrotheca* mostly occur as scattered individuals on the cliff faces, particularly on the south side of the island. The annual *Phacelia distans* forms several large localized colonies near the base of the southern cliff, and the perennial *Stephanomeria elata* was represented by only a few plants growing on rocky slopes at the extreme eastern end of the island. A few scattered individuals of an unidentified *Arbutus* occur on the plateau, but their distribution, short stature, and much-branched condition suggest that these were planted and are not the native *A. menziesii*.

Numerous lichens are present on the soil, rocks, and especially on the trees. These include *Flavopunctelia flaventior*, *Physcia callosa*, *Punctelia subrudecta*, *Rinodina* sp., and *Xanthoria polycarpa*. Terrestrial and epiphytic bryophytes are also common but were not identified.

WEST MARIN ISLAND

The forest on West Marin Island is depauperate compared with that on East Marin Island. On the western portions of this island, *Quercus agrifolia* and *Heteromeles arbutifolia* occur as shrubs interspersed with *Rosa gymnocarpa* in a matrix of annual introduced grasses. The eastern portion is dominated by larger individuals of the oak and *H. arbutifolia*, but also includes *Sambucus mexicana*. Several of the trees in this eastern area are infested by *Hedera helix*. The central and northern slopes of the island support the best developed forest, where the dominant tree is *Aesculus californica*. Several large, spreading buckeyes of obvious antiquity occupy this area. They are the favored nesting sites for the Black-crowned Night Heron (*Nycticorax nycticorax*), Snowy Egret (*Egretta thula*), Great Egret (*Casmerodium albus*), and Great Blue Heron (*Ardea herodias*). Their major branches are cloaked with twiggy nest platforms. Some individuals of *Quercus agrifolia* occur in this area as well but they are

dwarfed by the buckeyes. The understory directly beneath the buckeyes is essentially bare, perhaps due to the influence of the nesting birds. In these areas, nests of the Canada Goose (*Branta canadensis*) are found. We did not observe nesting of the Western Gull (*Larus occidentalis*), but it apparently nests on relatively open sites.

Northern coastal scrub on West Marin Island occurs in two distinct phases. The southern and eastern margin of the island is dominated by *Artemisia californica* with very few shrubs of *Mimulus aurantiacus*. The cliffs in this area also host *Dudleya cymosa*, *Eriogonum nudum*, and the introduced *Sonchus oleraceus*. In contrast, northern coastal scrub elements along the western and northern margins of the island include *Baccharis pilularis* and *Eriophyllum staechadifolium*. Northside cliffs also host *Scrophularia californica* and *Polypodium californicum*.

Coastal salt marsh elements occur sporadically in the zone where the cliffs meet the cobble beach that fringes the island. For example, a small patch of *Frankenia salina* occurs at the eastern tip of the island. *Spergularia macrotheca* is found in cliff crevices near the water line on the northern margin of the island. *Salicornia virginica* occurs more generally in this habitat.

COMPARISON OF THE TWO ISLANDS

There are notable vegetational and floristic differences between West Marin and East Marin islands. The plateau on West Marin Island is dominated in winter and spring by a very dense sward of introduced annual grasses. On the northern side of the plateau and the slopes below it *Bromus diandrus* predominates and on the southern side of the plateau and the slopes below it *Avena fatua* predominates. These grasses dominate most areas where soil has formed on the plateau and down the cliff sides. While these grasses are not normally considered nitrophiles, they thrive on the guano-enriched soils to the exclusion of most other introduced and native vascular plants. Recruitment of the major tree and shrub species appears to be virtually nil on this island. Both grasses also occur on East Marin Island, but only on the extreme eastern tip of that island, where birds (apparently mostly Canada Geese) congregate but do not nest, do they form the dense stands seen on West Marin Island.

The soil under the trees in which the birds roost and nest on West Marin Island is bare, probably due to a combination of shading and extreme guano enrichment. Anderson (1960) attributed these bare areas to guano deposits. There are also occasional bare areas in the grasslands that appear to be induced by the physical presence of (but not the nesting of) birds. In places, grasses had been uprooted by birds, perhaps during the course of courtship, territorial displays, or nest-building. The bare soil under *Aesculus californica* was littered

with green branch tips during a visit in mid-March. These appear to have been clipped by the Black-crowned Night Herons and Great Egrets that were beginning to nest. The long-term effect of this pruning on the growth pattern of the trees is uncertain.

Three herbaceous species that are extremely abundant on East Marin Island appear to be absent from West Marin Island: *Sanicula crassicaulis*, *Stachys ajugoides* var. *rigida*, and *Dryopteris arguta*. *Claytonia perfoliata* and *Polypodium californicum*, both common on East Marin Island, are sparingly represented on West Marin Island. The woody *Lonicera hispidula* var. *vacillans* and *Symporicarpos albus* var. *laevigatus*, both common on East Marin Island, appear to be missing from West Marin Island. In contrast, *Scrophularia californica* competes very well with the introduced annual grasses and is probably more abundant per unit area on West Marin Island than on East Marin Island.

We were struck by these striking vegetational and floristic differences between the two islands, differences that we believe are due to the prolonged presence of large numbers of birds on West Marin Island but not on East Marin Island. As described above, these birds apparently have important effects on plant life by the physical disturbances they cause and, more important, by alterations of soil chemistry due to deposition of guano. Striking effects of seabird occupancy on the vegetation and flora of oceanic islands have been noted (Ornduff 1965; references in Vasey 1990). With the exception of the few primarily floristic studies of the Farallon Islands (Ornduff 1961; Coulter 1971, 1978; Vasey 1990), the vegetation and flora of the coastal islands of California harboring extensive seabird rookeries appear to be unstudied. Since humans no longer reside on East Marin Island and human visitation to both Marin islands is now highly restricted, we suspect that soon most if not all the bird species that nest on West Marin Island will begin to nest on East Marin Island. If this happens, and our surmise about the impact of these birds on the plant life of West Marin Island is correct, vegetational and floristic patterns on East Marin Island will begin to change. Although our studies are not quantitative, we hope our observations on the present vegetation and flora of both islands will provide a stimulus for others to conduct quantitative investigations in the near future and to monitor possible biotic changes on East Marin Island in the next few decades.

ACKNOWLEDGMENTS

We are grateful to Richard Spight, Elena Spight, and Michael McCarthy for facilitating visits to the Marin Islands, Travis Columbus for identification of the grasses, William Culberson for identification of the lichens, John West for identification of the alga, Leslie Gottlieb for identification of the *Stephanomeria*, and Kris Albert for locating a copy of the Kroll report.

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(Received 23 Aug 1994; accepted 18 Nov 1994)

NATIVE VASCULAR PLANTS OF THE MARIN ISLANDS

The known native vascular flora of the two islands consists of 65 species. Twenty-six of these are known from both islands, 37 are known only from East Marin Island, and two were collected only on West Marin Island. Doubtless we overlooked several native and introduced species during our visits. The nomenclature in the appended list follows that used in *The Jepson Manual: higher plants of California* (Hickman 1993). (W = recorded on West Marin Island, E = recorded on East Marin Island):

FLOWERING PLANTS

- Achillea millefolium* L. (Asteraceae) E
- Aesculus californica* (Spach) Nutt. (Hippocastanaceae) W, E
- Amsinckia* sp. (Boraginaceae) E
- Artemisia californica* Less. (Asteraceae) W, E
- Artemisia douglasiana* Besser (Asteraceae) E
- Baccharis pilularis* DC. (Asteraceae) W, E
- Brodiaea californica* Lindl. var. *californica* (Liliaceae) E
- Calystegia purpurata* (E. Greene) Brummitt ssp. *purpurata* (Convolvulaceae) E
- Camissonia ovata* (Torr. & A. Gray) Raven (Onagraceae) E
- Carex barbae* Dewey (Cyperaceae) E
- Chlorogalum pomeridianum* (DC.) Kunth var. *pomeridianum* (Liliaceae) W, E
- Clarkia rubicunda* (Lindl.) H. Lewis & M. Lewis (Onagraceae) W
- Claytonia perfoliata* Willd. ssp. *perfoliata* (Portulacaceae) W, E
- Cressa truxillensis* Kunth (Convolvulaceae) E
- Cynoglossum grande* Lehm. (Boraginaceae) E
- Dichelostemma capitatum* Alph. Wood ssp. *capitatum* (Liliaceae) E
- Dichondra donelliana* Tharp & M. Johnston (Convolvulaceae) E
- Distichlis spicata* (L.) E. Greene (Poaceae) W, E

Dudleya cymosa (Lemaire) Britton & Rose ssp. *paniculata* (Jeps.) K. Nakai (Crassulaceae) W, E
Eriogonum nudum Benth. var. *nudum* (Polygonaceae) W, E
Eriophyllum staechadifolium Lagasca (Asteraceae) W, E
Eschscholzia californica Cham. (Papaveraceae) W, E
Festuca californica Vasey (Poaceae) W
Frankenia salina (Molina) I.M. Johnston (Frankeniaceae) W, E
Gnaphalium canescens DC. (Asteraceae) E
Gnaphalium stramineum Kunth (Asteraceae) E
Heteromeles arbutifolia (Lindley) Roem. (Rosaceae) W, E
Holodiscus discolor (Pursh) Maxim. (Rosaceae) W, E
Iris sp. (Iridaceae) E
Jaumea carnosa (Less.) A. Gray (Asteraceae) E
Lathyrus sp. (Fabaceae) W, E
Lomatium utriculatum (Torr. & Gray) J. Coulter. & Rose? (Apiaceae) E
Lonicera hispidula Douglas var. *vacillans* A. Gray (Caprifoliaceae) E
Lotus scoparius (Nutt.) Ottley var. *scoparius* (Fabaceae) W, E
Lupinus nanus Benth. (Fabaceae) E
Luzula comosa E. Meyer (Juncaceae) E
Melica torreyana Scribner (Poaceae) E
Mimulus aurantiacus Curtis (Scrophulariaceae) W, E
Nassella lepida (A. Hitchc.) Barkworth (Poaceae) E
Nassella pulchra (A. Hitchc.) Barkworth (Poaceae) E
Triphysaria pusilla (Benth.) Chuang & Heckard (Scrophulariaceae) E
Phacelia distans Benth. (Hydrophyllaceae) E
Polycarpon depressum Nutt. (Caryophyllaceae) E
Quercus agrifolia Nee (Fagaceae) W, E
Rosa gymnocarpa Nutt. (Rosaceae) W, E
Rumex salicifolius J.A. Weinm. var. *crassus* (Rech.f.) J. Howell (Polygonaceae) E
Ruppia maritima L. (Potamogetonaceae) E
Salicornia virginica L. (Chenopodiaceae) W, E
Sambucus mexicana C. Presl (Caprifoliaceae) W, E
Sanicula crassicaulis DC. (Apiaceae) E
Scrophularia californica Cham. & Schlecht. ssp. *californica* (Scrophulariaceae)
W, E
Spergularia macrotheca (Hornem.) Heynh. var. *macrotheca* (Caryophyllaceae)
W, E
Stachys ajugoides Benth. var. *rigida* Jeps. & Hoover (Lamiaceae) E
Stephanomeria elata Nutt. (Asteraceae) E
Symporicarpus albus (L.) S.F. Blake var. *laevigatus* (Fern.) S.F. Blake (Caprifoliaceae) E
Toxicodendron diversilobum (Torr. & A. Gray) E. Greene (Anacardiaceae) W, E
Umbellularia californica (Hook. & Arn.) Nutt. (Lauraceae) W, E
Vicia americana Willd. var. *americana* (Fabaceae) Vetch E
Viola pedunculata Torr. & A. Gray (Violaceae) E
Zigadenus fremontii (Torr.) S. Watson (Liliaceae) W, E

FERNS

Adiantum jordanii C. Mueller (Pteridaceae) E
Dryopteris arguta (Kaulf.) Maxon (Dryopteridaceae) E
Pentagramma triangularis (Kaulf.) G. Yatskievych, M.D. Windham & E. Wollenweber ssp. *triangularis* (Pteridaceae) E
Polypodium californicum Kaulf. (Polypodiaceae) W, E

VALLEY PEATLAND FLORA OF IDAHO

ROBERT J. BURSIK¹ and DOUGLASS M. HENDERSON
Department of Biological Science, University of Idaho,
Moscow, ID 83843

ABSTRACT

Twenty-eight low elevation peatlands in Idaho and northeastern Washington were surveyed for their flora. The flora contains 20 bryophyte and 291 vascular species, 62% of the species are boreal, 22% are western cordilleran, and 16% are widespread. Although most species are of boreal affinity, the Idaho peatland flora has relatively low similarity to other peatland floras in North America. The low similarity may be explained in part by the lack of trees and ericaceous shrubs in Idaho peatlands, and the relatively unknown status of Idaho's bryophyte flora. Five species, previously unknown for Idaho, were documented as peatland inhabitants: *Carex chordorrhiza*, *Eleocharis tenuis*, *Eriophorum viridicarinatum*, *Iris versicolor*, and *Rubus pubescens*.

Floristic and phytogeographic studies of peatlands have been conducted in many parts of boreal and northern temperate North America (Glaser and Foster 1984 in Labrador; Jeglum 1971 in Saskatchewan; Moss 1953 in Alberta; Janssens 1967 and Wheeler et al. 1983 in Minnesota; Lesica 1986 in Montana). Floristic and phytogeographic trends and interrelationships among northern temperate and boreal peatlands have also been documented from numerous studies of peatland vegetations (Slack et al. 1980 and Vitt et al. 1975 in Alberta; Damman and Dowhan 1981 in Nova Scotia; Pollett and Bridgewater 1973 and Wells 1981 in Newfoundland; Jeglum 1975 and Vitt and Bayley 1984 in Ontario; Ovenden and Brassard 1989 in the Yukon; Schwintzer and Williams 1974, Vitt and Slack 1975, and Schwintzer 1978a, b in Michigan; Glaser 1983, in Minnesota; Damman and French 1987, Dunlop 1987, Karlin and Lynn 1988, Motzkin and Patterson 1991, and Mitchell and Niering 1993 in the northeastern U.S.; Stewart and Nilsen 1993 in Appalachia). Peatlands of Idaho, however, escaped intensive floristic and phytogeographic study until the study of Bursik (1990). Only one vegetational study (Rumley 1956) from this region (Hager Lake in Bonner Co., Idaho) had been accomplished prior to 1990. The vegetation and flora of Hager Lake were reanalyzed in 1992 to document changes during the last four decades.

Bursik (1990) recognized two broad types of peatlands in the northwestern Rocky Mountains based on vascular floristics: subalpine peatlands that generally form along low gradient streams and

¹ Present address: Idaho Conservation Data Center, Idaho Fish & Game, P.O. Box 25, Boise, ID 83707.

around lakes at mid- to high elevations, and low elevation lacustrine peatlands which typically form around lakes in large river valleys in parts of this region. This study focuses on the latter. We refer to these low elevation peatlands as valley peatlands, in recognition of their position on the landscape, regardless of the presence of a lacustrine open body of water, which is present in most, but not all of the study sites. Valley peatlands are dominated by boreal species which range through all or part of the northern boreal regions. Sub-alpine peatlands are characterized by numerous cordilleran species which are generally restricted to the ranges of mountains in western North America. Valley peatlands support relatively few cordilleran species.

The current study includes bryophytes as well as vascular plants, whereas the previous study by Bursik (1990) included only vascular species. Ordination studies undertaken throughout Canada indicate that bryophyte species respond to water chemistry changes and are, therefore, most valuable in elucidating local conditions which may shape species composition and abundance (Horton et al. 1993).

STUDY AREA DESCRIPTION

The study sites include 26 in Idaho and two in Pend Oreille County, Washington (Table 1). Both Washington sites are in the Priest River Valley, which drains half of the extreme northern Panhandle of Idaho, and supports the majority of valley peatlands in Idaho. The 28 sites represent a general north-south transect ($48^{\circ}, 46'$ in Boundary County, to $44^{\circ}, 02'$ in Fremont County) through the peatland-supporting portion of Idaho (Fig. 1). The sites range in elevation from 641 meters at Gamble Lake to 2000 meters at Robinson Lake (Table 1). Elevation increases along the transect from north to south. Legal locations of the study sites are also shown in Table 1.

Because of the latitudinal, elevational, and physiographic diversity of the region, it is difficult to characterize the climate of the valley peatland regions of Idaho. The climate of the Priest River Valley of northern Idaho, which supports the greatest concentration of valley peatlands in the state, has been described as "inland maritime" due to the prevailing westerlies, which carry air masses from the northern Pacific Ocean across the northern Rocky Mountains. Mean annual precipitation for the Priest River Experimental Forest in the southern part of the Priest River Valley is 81.3 cm, most of which occurs during the winter in the form of snow. The mean annual temperature is 6.8°C with a mean temperature of 18.2°C in July and -4.6°C in January (Cooper et al. 1987). The rest of the peatland regions of Idaho are similar, but somewhat drier and cooler in the higher elevations of the southern part of the study area.

TABLE 1. LOCATION, ELEVATION, AND LATITUDE OF 28 VALLEY PEATLAND STUDY SITES IN IDAHO AND WASHINGTON, U.S.A. Sites are listed in numerical sequence from north to south. S = Section, T = Township, R = Range. Legal locations without sections are unsurveyed.

Site & Number	County	Legal location	Elevation (m)	Latitude
Upper Priest Lake (1)	Bonner	S33 T63N R4W	790	48°46'
Mosquito Bay (2)	Bonner	S10 T62N R3W	752	48°45'
Armstrong Meadows (3)	Bonner	S5 T62N R4W	794	48°45'
Bottle Lake (4)	Bonner	S20 T62N R4W	872	48°45'
Perkins Lake (5)	Boundary	S5 T62N R3E	810	48°45'
Huff Lake (6)	Pend Orielle	S15 T36N R45W	820	48°44'
Packer Meadows (7)	Bonner	S21 T62N R5W	1120	48°42'
Rose Fen (8)	Boundary	S3 T61N R3E	751	48°40'
Three Ponds (9)	Boundary	S14 T61N R1W	1124	48°37'
Potholes (10)	Bonner	S20 T61N R5W	900	48°36'
Deerhorn Cr. Meadows (11)	Pend Orielle	S15 T36N R45W	920	48°36'
Hager Lake (12)	Bonner	S34 T61N R5W	800	48°36'
MacArthur Lake (13)	Boundary	S27 T60N R1W	642	48°30'
Lee Lake (14)	Bonner	S11 T59N R4W	762	48°20'
Chase Lake (15)	Bonner	S14 T59N R4W	768	48°27'
Kaniksu Marsh (16)	Bonner	S25 T59N R4W	738	48°26'
Chippmunk Potholes (17)	Bonner	S31 T59N R4W	740	48°25'
Gamble Lake (18)	Bonner	S7 T56N R1E	641	48°13'
Shepherd Lake (19)	Bonner	S23 T56N R2W	702	48°11'
Rose Lake (20)	Kootenai	S33 T49N R1W	653	47°33'
Lily Lake (21)	Valley	S27 T19N R3E	1527	44°57'
Tule Lake (22)	Valley	S13 T15N R6E	1630	44°37'
Big Springs (23)	Fremont	S33 T13N R44E	1963	44°30'
Genital Meadows (24)	Fremont	T10N R46E	1994	44°10'
Robinson Lake (25)	Fremont	T10N R46E	2000	44°10'
West Boundary Trail Meadows (26)	Fremont	T10N R45E	1994	44°08'
Rock Creek Potholes (27)	Fremont	S10 T9N R45E	1965	44°08'
Indian Lake (28)	Fremont	S32 T9N R46E	1963	44°04'

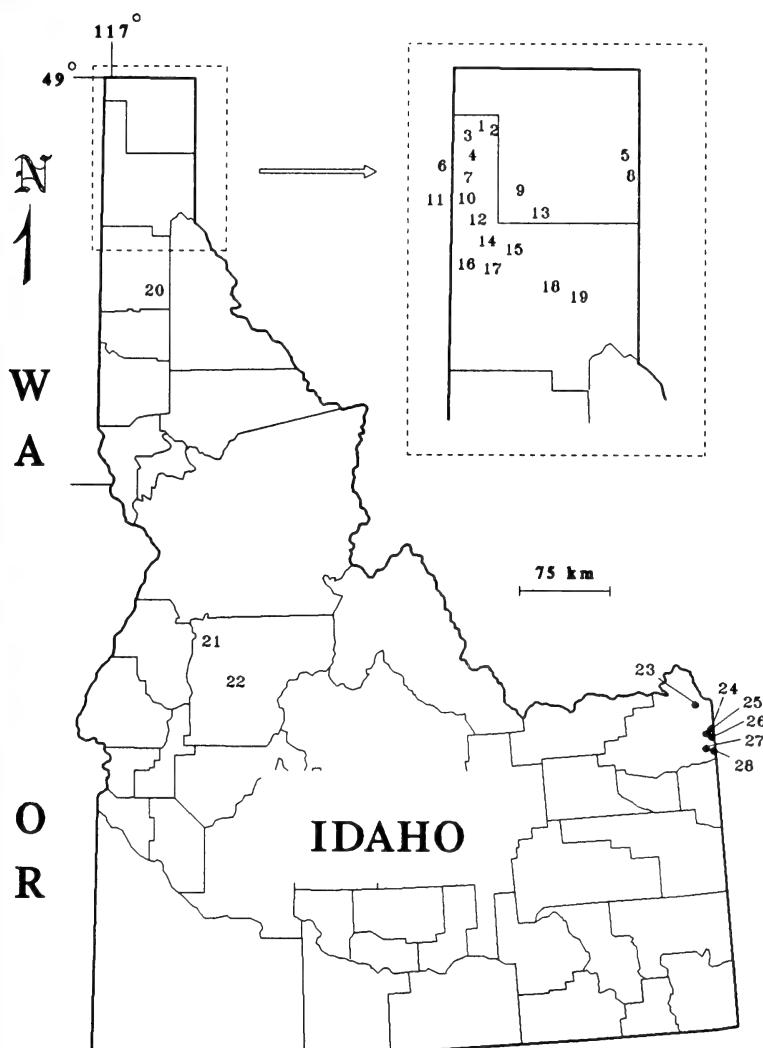


FIG. 1. Location of 28 peatland study sites in Idaho and adjacent northeastern Washington. Study sites and numbers are listed in Table 1.

The uplands adjacent to valley peatlands in northern Idaho and northeastern Washington are dominated by western temperate coniferous forests characterized by *Larix occidentalis*, *Pseudotsuga menziesii*, *Pinus contorta*, *P. ponderosa*, *P. monticola*, *Abies grandis*, *Tsuga heterophylla*, and *Thuja plicata*. *Pinus contorta*, *P. ponderosa*, and *Pseudotsuga menziesii* are dominant in the southern part of the study region. Valley peatlands occur in cirques, glacial kettles, glacial

scours, and glacial outwash channels, and are the product of continental Pinedale Wisconsin glacial activity (Rabe et al. 1986).

The 28 study sites represent predominantly *Sphagnum*-rich peatlands with oligotrophic ground waters (Horton et al. 1993). Several sites, e.g., Rose Fen, are *Sphagnum*-poor peatlands, dominated by brown mosses, sedges, and other graminoids. In the traditional sense, the *Sphagnum*-rich peatlands are fens, ranging from poor fens to moderately rich (mesotrophic) fens. Several of the poor fen sites (e.g., Chase Lake and Huff Lake) include localized raised bog (ombrotrophic) habitats dominated by *Sphagnum fuscum*, although the rich floras of each of these areas, considered as a whole, indicate the presence of predominantly poor fen conditions.

METHODS

Twenty-eight sites, selected to represent a diversity of valley peatlands in Idaho, and adjacent Washington were studied from 1987 to 1993. Most of the peatlands are located on federal lands and several are included within Research Natural Areas (Table 1).

Most study sites were visited at different times during the growing season to document phenological changes in the vascular flora. Terrestrial (mat) habitats were surveyed extensively on foot. Open water was covered by canoe, inflatable raft, or by wading. To account for as much floristic diversity as possible, particular attention was given to habitats characterized by different types of vegetation, various degrees of microtopographic relief, and varied patterns of drainage.

The establishment of peatland boundaries for sampling was based on the presence of moist to wet peat soils dominated by peat mosses, brown mosses (e.g., *Aulacomnium palustre* and *Calliergon stramineum*), sedges and other characteristic wetland taxa. The narrow transition from peat to predominantly mineral soils supporting upland trees was considered the peatland boundary. Extensive paludified forest exists in several of the sites (e.g., Mosquito Bay, Armstrong Meadows, Lee Lake). Upland tree species such as *Tsuga heterophylla* and *Pinus contorta* were included in the species lists if they occurred on peat or on thick mats of *Sphagnum centrale*. Although no tree species are specifically adapted to peatland habitats in the region, most of the locally dominant conifers occur in the paludified habitats and scattered on raised hummocks in other, non-paludified portions of the peatlands.

Over 2000 voucher specimens were collected to document this study and are deposited in the University of Idaho Herbarium (ID). Data from these collections and specimens already on deposit in ID were used in compiling floristic lists for each study area. Nomenclature follows Hitchcock and Cronquist (1973) and Moss (1959) for Angiosperms, Flora of North America Editorial Committee (1993)

for Pteridophytes and Gymnosperms, Lawton (1971) for non-*Sphagnum* bryophyte species, and Andrus and Layser (1976) for *Sphagnum* spp.

Sorenson's Index of Similarity, with the formula: $S = (2w/a + b) \times 100$, where w is the number of species in common between two areas, and a and b are the number of species in areas A and B, respectively, was used to compare the valley peatland flora of Idaho with other regional peatland floras in North America. Sorenson's Index has been used in other phytogeographic studies (e.g., Wheeler et al. 1983; Lesica 1986). All comparisons were done at the species level. Species lists from other geographic regions in North America were compiled from the following studies: Lesica (1986) for north-central Montana; Jeglum (1975) and Vitt and Bayley (1984) for Northern Ontario; Vitt and Slack (1975), and Schwintzer (1978b) for northern Michigan; Damman and French (1987) for the Northeastern U.S.; Glaser (1983) for northern Minnesota; Wheeler et al. (1983) for the Red Lake Peatland in Minnesota; Jeglum (1971) for Saskatchewan; and Moss (1953), Slack et al. (1980), and Vitt et al. (1975) for Alberta.

RESULTS

The valley peatland flora of the northwestern Rocky Mountains consists of 311 species, 20 bryophytes and 291 vascular (Table 2). The Cyperaceae is the most prominent vascular family with six genera and 46 species, accounting for 15% of the flora. *Carex* with 32 species and *Sphagnum* with 11 species are the most important genera in the flora.

One hundred ninety-three of the 311 species (62%) are boreal in distribution, most of which are at or near their southern limit in Idaho. Sixty-nine species (22%) have ranges centered in the western cordillera of North America, and 49 species (16%) are widespread in North America or cosmopolitan in distribution (Table 2). The last group also includes introduced weeds of wide or local distribution in North America.

Thirty species (10%) in the valley peatland flora are considered rare in Idaho (Moseley and Groves 1992). Five of these species were undocumented in Idaho prior to this study: *Carex chordorrhiza*, *Eleocharis tenuis*, *Eriophorum viridicarinatum*, *Iris versicolor*, and *Rubus pubescens*.

Forty-four of the 69 cordilleran species (64%) occur in three or fewer sites. Most of these species occur on moist, minerotrophic margins in areas otherwise characterized by poor fen conditions. Other cordilleran species are characteristic of dried or disturbed habitats within the peatlands. Very few of the cordilleran species occur on fixed or floating mat locations on deep peat. Exceptions

TABLE 2. CHECKLIST OF VASCULAR PLANT SPECIES IN PEATLANDS OF IDAHO. P = phytogeographic affinity (b = boreal; w = western cordilleran; c = cosmopolitan or widespread North American); x = present, o = absent; 1 = Upper Priest Lake Fen; 2 = Perkin's Lake; 3 = Mosquito Bay; 4 = Bottle Lake; 5 = Armstrong Meadows; 6 = Huff Lake; 7 = Packer Meadows; 8 = Rose Fen; 9 = Three Ponds; 10 = Potholes; 11 = Deethorn Lake; 12 = Hager Lake; 13 = MacArthur Lake; 14 = Chase Lake; 15 = Lee Lake; 16 = Kaniksu Lake; 17 = Chipmunk Potholes; 18 = Gammel Lake; 19 = Shephard Lake; 20 = Rose Lake; 21 = Lily Lake; 22 = Tule Lake; 23 = Henry's Fork Fen; 24 = Gentian Meadow; 25 = Robinson lake; 26 = West Boundary Creek Meadow; 27 = Rock Creek Potholes; 28 = Indian Lake. Nomenclature follows Hitchcock and Cronquist (1973) or Moss (1959) for Angiosperms; Flora of North America Editorial Committee (1993) for Pteridophytes and Gymnosperms; Andrus and Layser (1976) for *Sphagnum*; and Lawton (1971) for other bryophytes.

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	P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Asteraceae																													
<i>Anaphalis margaritacea</i> (L.) Britt.	b	o	x	o	o	o	o	o	x	o	o	x	o	x	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Antennaria microphylla</i> Rydb.	w	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o
<i>Arnica amplexicaulis</i> Nutt. <i>Arnica latifolia</i> Bong.	w	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Aster eatonii</i> (Gray) Howell <i>Aster foliaceus</i> Lindl.	w	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Aster junceiformis</i> Rydb. <i>Aster modestus</i> Lindl.	b	o	x	o	o	o	o	o	x	o	o	x	o	x	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Bidens cernua</i> L. <i>Bidens vulgata</i> Greene	b	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	x	x	o	o	x	x	o	o	o	o
<i>Cirsium arvense</i> (L.) Scop. <i>Cirsium vulgare</i> (Savi) Tenore	c	o	o	o	o	o	o	o	o	x	o	x	o	x	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Erigeron peregrinus</i> (Pursh) Greene	w	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o
<i>Helianthella uniflora</i> (Nutt.) T. & G.	w	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o
<i>Hieracium albiflorum</i> Hook.	w	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Petasites sagittatus</i> (Banks) Gray	b	o	x	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Senecio hydrophilus</i> Nutt. <i>Senecio inaequior</i> Greene	w	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Senecio triangularis</i> Hook. <i>Solidago canadensis</i> L.	w	o	x	o	o	o	o	o	x	o	o	x	o	x	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o
<i>Tanacetum vulgare</i> L.	c	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	x	o	o	o	o	o
<i>Taraxacum officinale</i> Weber	c	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	x	o	o	o	o	o

TABLE 2. CONTINUED

	P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
Juncaceae																														
<i>Juncus acuminatus</i> Michx.	b	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o	
<i>Juncus alpinus</i> Vall.	b	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus balticus</i> Willd.	b	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o	
<i>Juncus brachyphyllus</i> Wieg.	w	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus effusus</i> L.	c	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus ensifolius</i> Wikst.	w	o	x	o	x	o	x	o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
<i>Juncus filiformis</i> L.	b	o	x	o	o	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus nevadensis</i> Wats.	w	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus nodosus</i> L.	b	o	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus tenuis</i> Willd.	c	o	o	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus tweedyi</i> Rydb.	w	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Juncus vaseyi</i> Engelm.	b	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
Juncaginaceae																														
<i>Triglochin maritima</i> L.	c	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	x	x	x	x	x	x	x	x
<i>Triglochin palustre</i> L.	b	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
Lamiaceae																														
<i>Lycopus americanus</i> Muhl.	c	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Lycopus uniflorus</i> Michx.	b	o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			
<i>Mentha arvensis</i> L.	b	o	o	o	o	o	o	o	x	o	x	o	x	o	x	o	x	o	x	o	x	o	x	o	x	o	x	x		
<i>Prunella vulgaris</i> L.	c	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
<i>Scutellaria galericulata</i> L.	b	o	x	o	o	x	o	o	x	o	o	x	o	o	x	o	o	x	o	o	o	o	o	o	o	o	o	o	o	
<i>Scutellaria laterifolia</i> L.	b	o	x	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
Leguminosae (s.l.)																														
<i>Trifolium repens</i> L.	c	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	
Lemnaceae																														
<i>Lemna minor</i> L.	b	o	o	o	x	o	o	x	o	o	o	x	o	o	x	o	o	x	o	o	x	o	o	x	o	o	o	o	o	
<i>Spirodela polyrhiza</i> (L.) Schleid.	b	o	o	o	x	o	o	o	o	o	o	x	o	o	x	o	o	x	o	o	x	o	o	x	o	o	o	o	o	

TABLE 2. CONTINUED

TABLE 3. SORENSEN'S INDEX OF SIMILARITY VALUES (S) FOR THE VALLEY PEATLAND FLORA OF IDAHO (WITH 311 SPECIES TOTAL) COMPARED WITH PEATLAND FLORAS FROM ELSEWHERE IN NORTH AMERICA. b = number of species on comparison flora; w = number of species in common.

Comparison flora and author(s)	b	w	S
Pine Butte Fen, Montana, U.S.A. (Lesica 1986)	102	54	26.2
Northwestern Alberta, Canada (Moss 1953; Slack et al. 1980)	247	98	35.1
Candle Lake, Saskatchewan, Canada (Jeglum 1971)	165	92	38.7
Red Lake Peatland, Minnesota, U.S.A. (Wheeler et al. 1983)	251	94	33.5
Northern Minnesota, U.S.A. (Glaser 1987)	297	94	30.9
Upper Great Lakes Region, U.S.A. (Crum 1988)	204	71	27.6
Northern Michigan, U.S.A. (Vitt and Slack 1975; Schwintzer 1978)	164	52	21.9
Northern Ontario, Canada (Jeglum 1975; Vitt and Bayley 1984)	84	36	18.2
Northeastern U.S.A. (Damman 1987)	155	28	12.0

include *Carex cusickii*, *Kalmia microphylla*, *Trientalis arctica*, and *Spiraea douglasii* (Table 2). The majority of the dominant species in the valley peatlands in Idaho are boreal, including *Sphagnum angustifolium*, *S. centrale*, *S. subsecundum*, *S. magellanicum*, *Carex lasiocarpa*, *C. utriculata*, *Dulichium arundinaceum*, *Drosera anglica*, *D. rotundifolia*, *Lycopus uniflorus*, *Menyanthes trifoliata*, *Potentilla palustris*, and *Scheuchzeria palustris*.

The valley peatland flora of Idaho was compared with peatland floras from elsewhere in North America using Sorenson's Index of Similarity (Table 3). Similarity values ranged from 12.0 for the Northeastern USA. to 38.7 for Candle Lake, Saskatchewan. Generally, the most distant comparison areas from Idaho were least similar (Northeastern USA; Northern Ontario; and Northern Michigan). Floristic similarity, however, did not necessarily increase with geographic proximity.

DISCUSSION

As is true with other northern temperate peatland floras, the valley peatland flora of Idaho contains few regional species adapted specifically to peatland habitats. Rather, the flora is comprised predominantly of boreal species at or near their southern range limits. This fact, however, makes the relatively low Similarity Index values between Idaho's valley peatland flora and other regional North American peatland floras somewhat surprising.

Water chemistries of valley peatlands in Idaho (Bursik 1990) fall within the range of water chemistry values given for *Sphagnum*-rich and *Sphagnum*-poor peatlands studied throughout North America (e.g., Vitt and Slack 1975; Schwintzer 1978a, b; Vitt and Bayley 1984). Although ombrotrophic habitats are localized and rare in valley peatlands of Idaho, poor, mesotrophic and rich fen conditions, as indicated by surface and subsurface water cation concentrations, alkalinity, pH, and conductivity values gathered at more than half of the study sites, are well-represented in the region (Bursik 1990). Additionally, fen habitats support far more species than do the ombrotrophic bog habitats (Wheeler et al. 1983), hence the lack of abundant bog habitat would exclude relatively few species from the region and could not alone account for the unique flora.

Lesica (1986) reported that floristic similarity with the flora of Pine Butte Fen decreased with increasing distance from Pine Butte Fen, and also decreased with decreasing pH of the peatland groundwater. The regional peatland floras nearest to Idaho are from Pine Butte Fen, Montana, and northwestern Alberta (Fig. 2). The two regions with peatland floras most similar to the peatland flora of Idaho, however, are the Candle Lake region of Saskatchewan, and Red Lake Peatland in northern Minnesota (Table 3). All of the studies except for Lesica (1986) represent a wide range of trophic diversity. The most distant comparison areas (northern Ontario, northern Michigan, and the Northeastern USA) were least similar to Idaho's valley peatland flora, otherwise no geographic trend is apparent. The surprisingly low floristic similarity with Pine Butte Fen, which is in the western cordillera, can perhaps be explained by the narrow range of chemical diversity of that area (minerotrophic fen), compared to the wide diversity of peatlands included in this study.

Several other factors may account for the overall lack of floristic similarity between the valley peatlands of Idaho and other regional peatlands examined. The most obvious source of uniqueness is the presence of 69 western cordilleran species which may be shared with only two of the comparison areas. Bryophyte diversity in Idaho is still poorly documented, which may account for the low similarity with other peatland floras. With the exception of the Pine Butte Fen flora, all other regional floras include thorough documentation of the bryophyte components. Most of those areas support more than 60 bryophyte species, whereas we documented only 20, all of which are boreal. Wheeler et al. (1983) noted an equal to greater similarity among bryophytes versus vascular species between Red Lake Peatland, Minnesota and other peatlands floras in North America and Europe. Further documentation of the bryophyte flora of valley peatlands in Idaho will likely produce more species in common with peatlands of other North American regions.

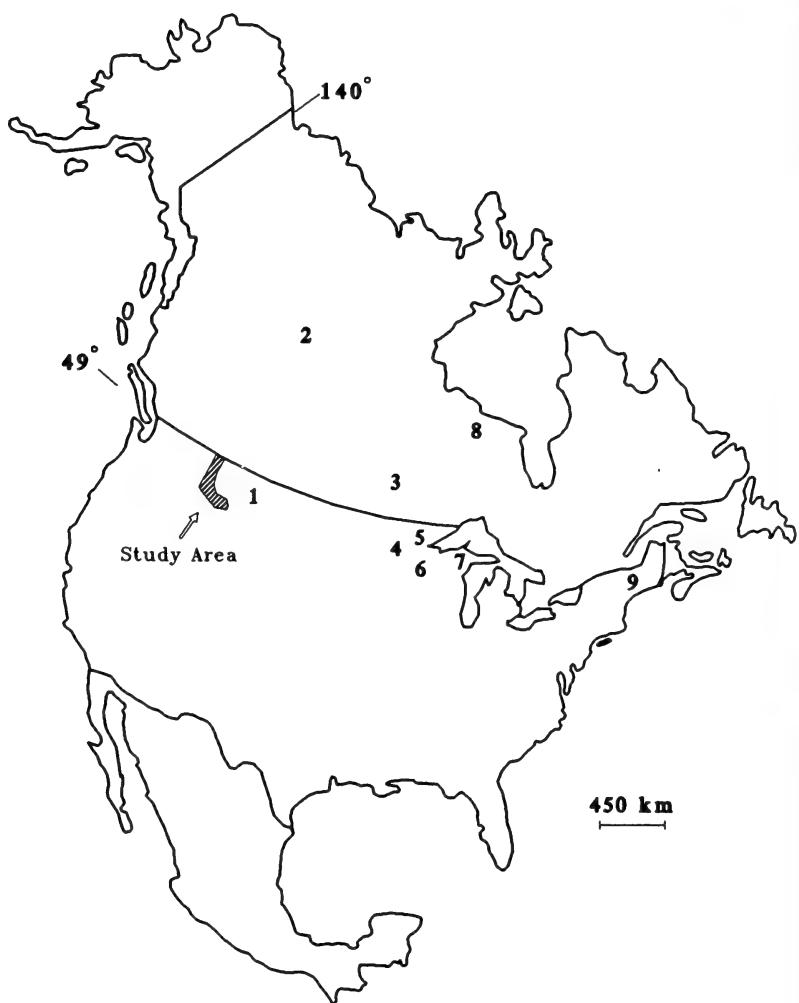


FIG. 2. North America with locations of study area in Idaho and regional peatland floras used for comparison. 1 = Pine Butte Fen, Montana; 2 = Northwestern Alberta; 3 = Candle Lake, Saskatchewan; 4 = Red Lake Peatland, Minnesota; 5 = Northern Minnesota; 6 = Upper Great Lakes Region; 7 = Northern Michigan; 8 = Northern Ontario; 9 = Northeastern USA. Publications from each of these sites are listed in Table 3.

We collected extensively in marginal minerotrophic to marshy areas and in aquatic habitats present within many of the study areas. These areas often support the greatest diversity of any habitat within a particular peatland due to mineral influences of adjacent uplands or inflowing streams. Most of the other regional studies from which

species lists were compiled were concerned only with true peatland habitats and did not include marginal habitats. Because many species in this flora are generally restricted to aquatic or marginal habitats, this also served to amplify differences between the Idaho valley peatland flora and other areas.

In boreal peatlands the three most important environmental factors influencing the development of peatland vegetation are trophic status of surface and groundwater, height of substrate surface above the water table, and degree of shading (Vitt and Bayley 1984; Vitt and Slack 1984; Kenel 1987). The first two factors also influence the abundance and distribution of species in Idaho's valley peatlands. Clearly, however, the absence of tree species adapted to peatlands must account for some of the uniqueness. Tree species adapted to peatland habitats account for the considerable physiognomic diversity of boreal peatland vegetation (Kenel 1987). Tree species such as *Picea glauca*, *P. mariana*, *Larix laricina*, *Thuja occidentalis*, and *Abies balsamea*, prominent components in boreal and other northern temperate peatlands, have no counterparts in valley peatlands in Idaho. Recently paludified forest habitats in Idaho are limited to the Priest River Valley, but the young age of these habitats, as evidenced by the shallow depth of the sphagnum mat and the persistence of tree species seemingly unsuited to such habitats, may not have allowed the development of a shade-tolerant portion of the flora that would accompany peatland tree species.

Unlike the peatlands of other North American regions, the valley peatlands of Idaho also lack a prominent ericaceous shrub component. *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Gaylussacia baccata*, and *Vaccinium vitis-idaea*, which can form dense shrub covers in boreal peatlands, have no counterpart in Idaho. The suite of conditions created by such shrub stands are largely absent from Idaho peatlands as are the species suited to those conditions.

ACKNOWLEDGMENTS

We thank Fred Rabe and Charles Wellner, who provided many helpful suggestions and for their critical reviews of an earlier version of the manuscript. Michael Curto and Steven Brunsfeld are acknowledged for assistance in identification of Poaceae and *Salix*, respectively. Special thanks go to Robert Moseley, who contributed much to this project through his collections and review of an earlier manuscript. Funding was provided by the C. R. Stillinger Trust, University of Idaho, during 1987–1988. Additional funding and support from 1991–1993 was provided by Idaho Fish and Game's Conservation Data Center in cooperation with the U.S. Forest Service.

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(Received 5 Jul 1994; accepted 7 Oct 1994)

NEW POACEAE DISTRIBUTION RECORDS FOR AGUASCALIENTES, MEXICO

MARGARITA DE LA CERDA-LEMUS

Centro Básico, Universidad Autónoma de Aguascalientes Avenida,
Universidad s/n, Aguascalientes, Ags., 20100, México

YOLANDA HERRERA-ARRIETA

CIIDIR Unidad Durango, COFAA-Instituto Politécnico Nacional,
Apartado Postal 738, Durango, Dgo., 34000, México

ABSTRACT

A floristic study of the family Poaceae from Aguascalientes, Mexico has been completed. Sixty-nine genera and 178 species were recorded, of which 43 are new records for the State, most of them from localities difficult of access in the Municipio of San José de Gracia. Taxa which represent new records are listed, along with habitat and distribution data for each.

RESUMEN

Se llevó a cabo un estudio florístico de la familia Poaceae en Aguascalientes, México. Se registraron 69 géneros y 178 especies, 43 de ellas resultaron ser nuevos registros para el Estado, muchos de ellos colectados en localidades de difícil acceso, en el Municipio de San José de Gracia. Se presenta un listado de estos taxa con datos adicionales sobre hábitat y distribución para cada taxón.

A floristic study of the State of Aguascalientes, Mexico is currently underway. Its primary objective is to update the knowledge of the flora. The family Poaceae is one of the largest in the world with about 620 genera and 10,000 species (Clayton and Renvoize 1986). We have recorded 69 genera and 178 species in Aguascalientes, many being indicators of disturbance, as well as serving as an important food source for livestock grazing.

The State of Aguascalientes is located in Central Mexico, between 21°38'03" and 22°07'06"N and 101°03'09" and 103°00'51"W. It is bounded by Zacatecas on the north, east and west sides and by Jalisco on the south. The State comprises an area of 5589 square km, divided into 9 Municipios (counties): Aguascalientes, Asientos, Calvillo, Cosío, Jesús María, Pabellón de Arteaga, Rincón de Romos, San José de Gracia y Tepezalá. The topography is uneven, consisting of a great central plain and a low mountainous region at the northwest. The altitude ranges from 1570 to 2900 m. The climate may be considered as semiarid, with some variation (de la Cerda and Si-queiros 1985).

The vegetation of Aguascalientes is xerophytic, predominantly secondary thorny shrub. *Quercus* and *Pinus* forests dominate the

mountains to the north, while southward there is a small region of tropical shrub. *Arctostaphylos pungens* shrub and grassland occur in small areas confined to the top of the higher mountains (de la Cerda and Siqueiros 1985).

Collections reported in this paper increase the floristic knowledge of Aguascalientes, and in general add to our knowledge of the grass flora of Mexico. Voucher specimens for these records are deposited in HUAA, with duplicates of some of them in CIIDIR, IEB, and ENCB.

RESULTS

Aegopogon cenchroides Humb. & Bonpl. ex Willd. (Eragrostideae: Cynodonteae). Municipio de Calvillo, arroyo Ojo de agua, Rancho El Tepozán, 1850 m, matorral subtropical, 5 Nov 90, *de la Cerda* 4080 (HUAA). Municipio San José de Gracia, bajío La Canoa, sierra de San Blas de pabellón, 2480 m, pastizal-bosque de *Juniperus* y *Quercus*, 15 Oct 90, *de la Cerda* 4089 (HUAA).

Previously known in Mexico from Baja California, Sonora, Chihuahua, Sinaloa, Nayarit, Jalisco, Colima, Michoacán, Guerrero, Guanajuato, México, Morelos, Distrito Federal, Hidalgo, Tlaxcala, Puebla, Veracruz, San Luis Potosí, Oaxaca, and Chiapas (McVaugh 1983; Beetle et al. 1983).

Agrostis hiemalis (Walt.) B.S.P. (Pooideae: Aveneae). Municipio de San José de Gracia, barranca Revientacuartas, rancho Los Alamillos, 2450 m, bosque de encino-pino, 12 Mar 90, *Rosales* c.310 (HUAA). Mpio. de Calvillo, El Tepozán, 1810 m, matorral subtropical, 30 Oct 89, HUAA, *de la Cerda* 3628 (HUAA, CIIDIR).

Previously known in Mexico from: Chihuahua, Durango, Jalisco, México, Distrito Federal, and San Luis Potosí (McVaugh 1983); Baja California, Sinaloa, Coahuila, Nuevo León, Guanajuato, Querétaro, Michoacán, Morelos, Oaxaca, and Chiapas (Beetle et al. 1983); and Puebla (Dávila et al. 1990).

Andropogon glomeratus (Walt.) B.S.P. (Panicoideae: Andropogoneae). Municipio de Pabellón de Arteaga, orilla del poblado, 1890 m, área de cultivo, 5 Nov 78, *Martinez* s.n. (HUAA).

Previously known in Mexico from Baja California, Durango, Nayarit, Jalisco, Michoacán, México, Oaxaca, Veracruz, Puebla, San Luis Potosí, Tamaulipas, Campeche, Quintana Roo, Yucatán and Chiapas (McVaugh 1983); Chihuahua, Coahuila, Nuevo León, Querétaro, Morelos, Distrito Federal, and Tabasco (Beetle et al. 1983).

Aristida mexicana Scribn. ex Henrard (Eragrostideae: Aristideae). Municipio de San José de Gracia, 6 km al W de San Antonio de los Ríos, 2550 m, manchón de encinos, 31 Aug 90, *de la Cerda* 3782 (HUAA, CIIDIR). Municipio de Calvillo, cerro Varas Verdes, 2000

m, matorral subtropical con disturbio, 20 Oct 90, *de la Cerda 4057* (HUAA). Mpio. Cosío 2 km al sur del rancho El Coyote, límite con Zacatecas, orilla de cultivo, 3 Sept 90, *de la Cerda 3005* (HUAA, CIIDIR).

Previously known in Mexico from Jalisco, Guanajuato, Puebla and Distrito Federal (Beetle et al. 1983).

Aristida ternipes Cav. var. *ternipes* (Eragrostideae: Aristideae). Municipio de San José de Gracia, bajío La Canoa, sierra de San Blas de Pabellón, 2480 m, pastizal natural en bosque de *Juniperus-Quercus*, 15 Oct 90, *de la Cerda 4107* (HUAA). Municipio de Calvillo, Las Bancas 1650 m, matorral subtropical, 24 Sept 88, *de la Cerda 3555* (HUAA). Municipio de Rincón de Romos, 2 km al SW de Pabellón de Hidalgo, 1950 m, matorral espinoso, 25 Aug 82, *de la Cerda 1609* (HUAA, CIIDIR).

Previously known in Mexico from Baja California, Sonora, Chihuahua, Durango, Sinaloa, Nayarit, Jalisco, Colima, Michoacán, Guanajuato, Guerrero, México, Morelos, Puebla, Veracruz, San Luis Potosí, Tamaulipas, Oaxaca, and Yucatán (McVaugh 1983); Tabasco and Quintana Roo (Beetle et al. 1983).

Arundo donax L. (Arundinoideae: Arundineae). Municipio de Aguascalientes, La Cantera, 1880 m, orilla de cultivo y canales de riego, 10 Oct 88, *de la Cerda 3363* (HUAA).

Previously known in Mexico from the Pacific Coast (McVaugh 1983); Baja California, Sonora, Chihuahua, Coahuila, Nuevo León, Tamaulipas, Sinaloa, Nayarit, San Luis Potosí, Guanajuato, Hidalgo, Distrito Federal, Puebla, Veracruz, Guerrero, Oaxaca, Chiapas, Campeche and Yucatán (Beetle et al. 1983); and Durango (González et al. 1991).

Bouteloua williamsii Swallen (Eragrostideae: Cynodoteae). Municipio Jesús María, 1880 m, matorral espinoso-manchón de encinos, 26 Sept 88, *de la Cerda 3334* (HUAA). Municipio de Aguascalientes, ladera NW del cerro El Picacho, 1980 m, matorral subinerme, 4 Sept 81, *de la Cerda 1006* (HUAA). Municipio de Calvillo, El Magüey, 1900 m, matorral subtropical, 24 Dec 79, Ruiz s.n. (HUAA). Municipio de San José de Gracia, 3 km al oeste de La Estancia, 2100 m, pastizal-matorral subtropical, 16 Aug 84, García 1832 (HUAA, CIIDIR).

Previously known in Mexico from Zacatecas, Nayarit, Jalisco, Guerrero, Oaxaca and Chiapas (McVaugh 1983; Beetle et al. 1983).

Calamagrostis pringlei Beal (Pooideae: Aveneae). Municipio de San José de Gracia, barranca Revientacuartas, rancho Los Alamitos, 2450 m, bosque de encino-pino, 12 Mar 90, Rosales C.311 (HUAA, IBUJAT).

Previously known in Mexico from Chihuahua, Nuevo León, Zacatecas and Hidalgo (Beetle et al. 1983).

Cynodon nemfuensis Vanderyst. (Chloridoideae: Cynodontae).

Municipio de Jesús María, 5 km al N de la Posta Zootecnica, 1880 m, matorral espinoso, 13 Dec 78, *Dávila s.n.* (HUAA).

Previously known in Mexico from Jalisco (McVaugh 1983); Veracruz, Tabasco and Yucatán (Beetle et al. 1983).

Dichanthium annulatum (Forsk.) Stapf (Panicoideae: Andropogoneae). Municipio de San José de Gracia, alrededores de la presa Jocoqui, 2230 m, matorral subtropical con disturbio, 25 Nov 78, *Negrete* 629 (HUAA).

Previously known in Mexico from Jalisco (McVaugh 1983); Chihuahua, San Luis Potosí, and Quintana Roo (Beetle et al. 1987).

Digitaria ciliaris (Retz.) Koeler (Panicoideae: Paniceae). Municipio de Calvillo, barranca El Temazcal, 1900 m, matorral subtropical, 16 Oct 89, *Garcia* 1976 (HUAA, CIIDIR). Municipio de Aguascalientes, La Cantera, 1880 m, orilla de cultivo, 10 Oct 88, *de la Cerdá* 3366 (HUAA). Minicipio de Jesús María, Los Arquitos, 1880 m, zona de disturbio, 26 Sept 88, *de la Cerdá* 3346 (HUAA).

Well known over much of the republic except Zacatecas and Tlaxcala (Beetle et al. 1987).

Digitaria insularis (L.) Mez ex Ekman (Panicoideae: Paniceae). Municipio de Tepezalá, cerro El Chivo, 2100 m, pastizal-matorral subinerme, 4 Sept 89, *de la Cerdá* 3473 (HUAA). Municipio de Cosío, 5 km al N de Zácatequillas, 1960 m, matorral espinoso, 7 Oct 83, *Siqueiros D.2499* (HUAA).

Previously known from almost the entire country except Baja California, Zacatecas, Aguascalientes, Michoacán, Morelos, Distrito Federal, Tlaxcala, and Tabasco (McVaugh 1983; Beetle et al. 1987).

Echinochloa jaliscana McVaugh (Panicoideae: Paniceae). Municipio de Aguascalientes, 50 m al N de Macario Gómez, 2000 m, orilla de camino, 12 Sept 88, *de la Cerdá* 3309 (HUAA).

Previously known from Jalisco, Guanajuato and Michoacán (McVaugh 1983); and Morelos (Beetle et al. 1991).

Elymus pringlei Scribn. and Merr. (Pooideae: Triticeae). Municipio de San José de Gracia, El Cibolo, 2630 m, claro en bosque de encino, 3 Sept 93, *Siqueiros D-4311* (HUAA).

Previously known in Mexico from Coahuila, Nuevo León, San Luis Potosí, Queretaro, Hidalgo, Morelos, Puebla, and Veracruz (Beetle et al. 1991).

Festuca breviglumis Swallen (Pooideae: Poeae). Municipio de San José de Gracia, mesa El Aparejo, sierra San Blas de Pabellón, 2450 m, pastizal-bosque de encino, 17 Aug 84, *García* 1886 (HUAA).

Previously known in Mexico from Jalisco (McVaugh 1983); Durango (Herrera 1988); Guanajuato, Morelos, Oaxaca and Chiapas (Beetle et al. 1991).

Ixophorus unisetus (Presl) Schlecht. (Panicoideae: Paniceae). Municipio de Aguascalientes, Peñuelas, 1880 m, a orilla de cultivo, 24 May 78, *Galindo s.n.* (HUAA).

Previously known in Mexico from Sinaloa, Jalisco, Guerrero, Morelos, Veracruz, and San Luis Potosí (McVaugh 1983); Nayarit, Colima, Michoacán, Guanajuato, Tamaulipas, Distrito Federal, Puebla, Oaxaca, and Chiapas (Beetle et al. 1991).

Lasiacis nigra Davidse (Panicoideae: Paniceae). Municipio de Calvillo, El Tepozán, 1810 m, orilla de arroyo, 30 Oct 89, *de la Cerda* 3629 (HUAA, CIIDIR). Barranca El Temazcal, 2.5 km al NW de la Labor, 1900 m, matorral subtropical, 16 Oct 89, *Ramirez s.n.* (HUAA, CIIDIR).

Previously known in Mexico from Tamaulipas, Nuevo León, Guanajuato, San Luis Potosí, Nayarit, Jalisco, Michoacán, Guerrero, México, Morelos, Hidalgo, Puebla, Veracruz, Oaxaca, and Chiapas (McVaugh 1983); Durango (Herrera 1986); Puebla, Distrito Federal, and Tabasco (Beetle et al. 1991).

Lolium temulentum L. (Pooideae: Poeae). Municipio de Aguascalientes, San Bartolo, 1884 m, orilla de cultivo, 22 May 79, *de Lira s.n.* (HUAA).

Previously known in Mexico from Baja California, Jalisco, and Veracruz (McVaugh 1983); San Luis Potosí, Puebla, and Oaxaca (Beetle et al. 1991).

Muhlenbergia brevivaginata Swallen (Chloridoideae: Eragrostideae). Municipio de San José de Gracia, Laguna Seca, 2520 m, bosque de encino-pino, 15 Feb 91, *Rosales 604* (HUAA).

Previously known in Mexico from Zacatecas and Jalisco (McVaugh 1983); and Durango (Herrera 1986).

Muhlenbergia ciliata (H.B.K.) Kunth (Chloridoideae: Eragrostideae). Municipio de Jesús María, mesa El Montoro, 2340 m, pastizal natural-bosque de encino, 8 Oct 90, *de la Cerda 3901* (HUAA). Municipio de San José de Gracia, alrededores de la presa Calles, 2100 m, matorral subinerme, 24 Aug 92, *de la Cerda 4359* (HUAA). Municipio de Calvillo, cerro Varas Verdes, 2000 m, matorral subtropical con disturbio, 29 Oct 90, *de la Cerda 4048* (HUAA, IEB).

Previously known in Mexico from Baja California Sur, Chihuahua, Sinaloa, Durango, Zacatecas, Jalisco, Michoacán, México, Morelos, Distrito Federal, Oaxaca, and Veracruz (McVaugh 1983); and Puebla (Dávila et al. 1990).

Muhlenbergia distans Swallen (Chloridoideae: Eragrostideae). Municipio de Cosío, El Zapote, 1 km al S de Cosío, 2000 m, matorral subinerme, 9 Sept 91, *de la Cerda 4194* (HUAA).

Previously known in Mexico from Durango, Zacatecas, Jalisco, Michoacán, México, Distrito Federal, Tlaxcala, Oaxaca, Hidalgo, Puebla, and San Luis Potosí (McVaugh 1983).

Muhlenbergia eriophylla Swallen (Chloridoideae: Eragrostideae). Municipio de San José de Gracia, lado SW de la presa La Araña, 2580 m, bosque de encino-pino, 14 Sept 81, *Garcia 1371* (HUAA).

Uncommon taxon, previously known in Mexico from México

State (Swallen 1950); Durango and Michoacán (Herrera and Grant 1993).

Muhlenbergia glauca (Nees) Mez (Chloridoideae: Eragrostideae). Municipio de San José de Gracia, Bajío La Canoa, sierra de San Blas de Pabellón, 2480 m, pastizal-bosque de *Juniperus*, 15 Oct 90, *de la Cerda* 4090 (HUAA). Municipio de Aguascalientes, cerro El Roble, 2080 m, matorral espinosos-nopalera, 30 Sept 91, *de la Cerda* 4225 (HUAA). Municipio de Jesús María, Los Arquitos, 1880 m, matorral espinoso con manchón de encinos, 26 Sept 88, *de la Cerda* 3331 (HUAA).

Previously known in Mexico from Chihuahua, Coahuila, San Luis Potosí, Guanajuato, Jalisco, and Distrito Federal (McVaugh 1983).

Muhlenbergia macrotis (Piper) Hitchc. (Chloridoideae: Eragrostideae). Municipio de Aguascalientes, ladera NE del cerro El Picacho, 2100 m, pastizal-manchón de encinos, 23 Sept 88, *de la Cerda* 3021 (HUAA). Municipio de San José de Gracia, barranca Los Hoyos, 2500 m, bosque de pino-encino, 17 Oct 88, *de la Cerda* 3405 (HUAA). Municipio de Calvillo, barranca Rio Gil, 1900 m, matorral inerme-bosque de encino, 21 Sept 92, *de la Cerda* 4409 (HUAA).

Previously known in Mexico from Sinaloa, Durango, Zacatecas, Nayarit, Guanajuato, Jalisco, Michoacán, Guerrero, Distrito Federal, Oaxaca and Puebla (McVaugh 1983; Beetle 1983).

Muhlenbergia quadridentata (H.B.K.) Kunth (Chloridoideae: Eragrostideae). Municipio de Tepezalá, 2 km al E de Tepezalá, 2200 m, pastizal, 24 Sept 90, *de la Cerda* 3896 (HUAA). Municipio de San José de Gracia, 6 km al W de San Antonio de los Ríos, 2550 m, manchón de encinos, 15 Oct 90, *de la Cerda* 4007 (HUAA). Municipio de Calvillo, 7 km al NW del Temazcal, 2300 m, bosque de encino, 29 Oct 90, *de la Cerda* 4973 (HUAA, CIIDIR).

Previously known in Mexico from Jalisco, Michoacán, México, Morelos, Distrito Federal, Tlaxcala, and Puebla (McVaugh 1983); Durango, Guanajuato, and Oaxaca (Herrera and Bain 1991).

Muhlenbergia rigens (Benth.) Hitchc. (Chloridoideae: Eragrostideae). Municipio de Calvillo, Puentes Cuates, 1900 m, matorral subtropical, 21 Sept 92, *de la Cerda* 4398 (HUAA).

Previously known in Mexico from Baja California, Chihuahua, Durango, and Jalisco (McVaugh 1983); and Puebla (Beetle 1983).

Muhlenbergia robusta (Fourn.) Hitchc. (Chloridoideae: Eragrostideae). Municipio de San José de Gracia, bajío La Canoa, 2480 m, pastizal en bosque de *Juniperus-Quercus*, 15 Oct 90, *de la Cerda* 4080 (HUAA).

Previously known in Mexico from Nayarit, Guanajuato, Jalisco, Michoacán, México, Morelos, Distrito Federal, Oaxaca, Veracruz, Puebla, and Chiapas (McVaugh 1983); and Durango (González et al. 1991).

Muhlenbergia watsoniana Hitchc. (Chloridoideae: Eragrostideae).

Municipio de San José de Gracia, Sierra Fria sin localidad definida, 2500 m, pastizal-bosque de encino, 3 Nov 78, Hernández s.n. (HUAA).

Previously known in Mexico from San Luis Potosí (Hitchcock 1935); Jalisco (McVaugh 1983); and Durango (Herrera 1988).

Oplismenus burmannii (Retz.) Beauv. (Panicoideae: Paniceae). Municipio de Calvillo, arroyo Cebolletas, 1850 m, matorral subtropical, 21 Oct 91, *de la Cerda* 4281 (HUAA, DACB).

Previously known in Mexico from Baja California Sur, Sonora, Chihuahua, Sinaloa, Durango, Nayarit, Guanajuato, Jalisco, Colima, Michoacán, Guerrero, México, Morelos, Distrito Federal, Oaxaca, Veracruz, Yucatán, and Chiapas (McVaugh 1983); and Puebla (Dávila et al. 1990).

Oplismenus hirtellus (L.) Beauv. (Panicoideae: Paniceae). Municipio de Calvillo, orilla de arroyo, Ojo de Agua, rancho El Tepozán, 1859 m, matorral subtropical, 5 Nov 90, *de la Cerda* 4078 (HUAA, IEB).

Previously known in Mexico from Baja California, Sonora, Jalisco, and Michoacán (McVaugh 1983); and Puebla (Dávila et al. 1990).

Otatea acuminata (Munro) Calderón & Soderstrom (Bambusoideae: Bambuseae). Municipio de Calvillo, arroyo Ojo de Agua, rancho El Tepozán, 1850 m, matorral subtropical, 5 Nov 90, *de la Cerda* 4079 (HUAA).

Previously known in Mexico from Sonora, Sinaloa, Nayarit, Jalisco, Michoacán, Guerrero, México, Morelos, Oaxaca, Puebla, and Veracruz (McVaugh 1983); and Durango (González et al. 1991).

Panicum maximum Jacq. (Panicoideae: Paniceae). Municipio de Calvillo, arroyo Cebolletas, 1850 m, matorral subtropical, 21 Oct 91, *de la Cerda* 4278 (HUAA).

Previously known in Mexico from Sinaloa, Nayarit, Jalisco, Colima, Guerrero, México, Morelos, Oaxaca, San Luis Potosí, Veracruz, Chiapas, Campeche, and Yucatán (McVaugh 1983); and Puebla (Dávila et al. 1990).

Paspalum hartwegianum Fourn. (Panicoideae: Paniceae). Municipio de Aguascalientes, La Cantera, 1880 m, orilla de cultivo, 10 Oct 88, *de la Cerda* 3364 (HUAA).

Previously known in Mexico from Sonora, Nuevo León, San Luis Potosí, Guanajuato, Jalisco, Michoacán, Morelos, Oaxaca, and Yucatán (McVaugh 1983), and Puebla (Dávila et al. 1990).

Paspalum pubiflorum Rupr. ex Fourn. (Panicoideae: Paniceae). Municipio de Jesús María, Los Arquitos, 1880 m, orilla de arroyo, 26 Sept 88, *de la Cerda* 3351 (HUAA). Municipio de Calvillo, arroyo Malpaso, 1750 m, vegetación riparia, 18 Sept 81, *de la Cerda* 1106 (HUAA). Municipio Rincón de Romos, 4 km al SW de Pabellón de Hidalgo, 1950 m, matorral espinoso, 25 Aug 82, García 1603

(HUAA). Municipio de Aguascalientes, alrededores de la presa El Muerto 1910 m, matorral subinerme, 17 Aug 92, *de la Cerda* 4339 (HUAA).

Previously known in Mexico from Baja California, Sonora, Chihuahua, Coahuila, Durango, Jalisco, Guanajuato, Queretaro, Michoacán, Guerrero, Oaxaca, Puebla, San Luis Potosí, Nuevo León, and Tamaulipas (McVaugh 1983).

Pennisetum crinitum (H.B.K.) Spreng. (Panicoideae: Paniceae). Municipio de Aguascalientes, orilla de la presa El Muerto, 1910 m, matorral subinerme, 17 Aug 92, *de la Cerda* 4326 (HUAA).

Previously known in Mexico from Durango, Nayarit, Jalisco, Michoacán, Guanajuato, México, Morelos, Distrito Federal, Veracruz, and Chiapas (McVaugh 1983); and Puebla (Dávila et al. 1990).

Piptochaetium brevicalyx (Fourn.) Ricker. (Pooideae: Stipeae). Municipio de San José de Gracia, mesa El Aguila, sierra de San Blas de Pabellón, 2550 m, pastizal-bosque de encino, 12 Jul 84, *García* 2263 (HUAA).

Previously known in Mexico from San Luis Potosí, Hidalgo, and México (Rzedowski & Rzedowski 1990), and Durango (González et al. 1991).

Piptochaetium virescens (H.B.K.) Parodi (Pooideae: Stipeae). Municipio de San José de Gracia, bajío La Canoa, sierra de San Blas de Pabellón, 2480 m, pastizal-bosque de *Juniperus-Quercus*, 15 Oct 90, *de la Cerda* 4109 (HUAA). Municipio de Calvillo, cerro Varas Verdes, 2000 m, matorral subtropical, 29 Oct 90, *de la Cerda* 4066 (HUAA, CIIDIR).

Previously known in Mexico from Zacatecas, Jalisco, Michoacán, Guanajuato, México, Distrito Federal, Hidalgo, Morelos, Tlaxcala, Puebla, Veracruz, Tamaulipas, Oaxaca, and Chiapas (McVaugh 1983).

Sorghastrum nutans (L.) Nash (Panicoideae: Andropogoneae). Municipio de San José de Gracia, barranca El Empinado, sierra de San Blas de Pabellón, 2520 m, bosque de encino, 15 Oct 92, *de la Cerda* 3942 (HUAA).

Previously known in Mexico from Sonora, Zacatecas, Guanajuato, Jalisco, Michoacán, Revillagigedo islands, Queretaro, Oaxaca, Veracruz, Puebla, San Luis Potosí, Tamaulipas, and Coahuila (McVaugh 1983); and Durango (González et al. 1991).

Sporobolus macrospermus Scribn. ex Beal (Chloridoideae: Eragrostideae). Municipio de Calvillo, 8 km al SW de Los Alisos, 2320 m, matorral inerme, 14 Oct 83, *Siqueiros* 2554 (HUAA).

Previously known in Mexico from Jalisco, Michoacán, Guerrero, México, Oaxaca, and Chiapas (McVaugh 1983).

Stipa tenuissima Trin. (Pooideae: Stipeae). Municipio de Tepezalá, 2 km al E de la mina San Pedro, 2180 m, pastizal-matorral subespinoso, 20 July 84, *Siqueiros* 2713 (HUAA).

Previously known in Mexico from Mexico State, Puebla, Veracruz (Rzedowski and Rzedowski 1990); Coahuila, Nuevo León, San Luis Potosí, Veracruz, and Puebla (Beetle 1983).

Tripsacum dactyloides (L.) L. (Paniceae: Andropogoneae). Municipio de Aguascalientes, cerro El Roble, 2080 m, matorral inerme-nopalera, 30 Sept 91, *de la Cerda* 4228 (HUAA). Municipio Rincón de Romos, rancho Tres Sauces, 1880 m, orilla de canal de irrigación, 7 Aug 90, *Rosales* 397 (HUAA). Municipio de Calvillo, orilla de arroyo en El Tepozán, 1700 m, matorral subtropical, 18 Sept 80, *García* 287 (HUAA).

Previously known in Mexico from Durango, Nayarit, Jalisco, Michoacán, Guerrero, México, Morelos, Distrito Federal, Oaxaca, Puebla, San Luis Potosí, Coahuila, Tamaulipas, and Chiapas (McVaugh 1983); Nuevo León (Beetle 1983); and Puebla (Dávila et al. 1990).

Trisetum deyeuxioides (H.B.K.) Kunth (Pooideae: Aveneae). Municipio de San José de Gracia, barranca El Empinado, 2520 m, bosque de encino, 15 Oct 90, *de la Cerda* 3965 (HUAA). Municipio de Calvillo, Los Pilares, 2450 m, bosque de encino, 17 Oct 88, *de la Cerda* 3414 (HUAA).

Previously known in Mexico from Chihuahua, Durango, Zacatecas, Guanajuato, Jalisco, Michoacán, Guerrero, México, Morelos, Distrito Federal, Oaxaca, Hidalgo, Veracruz, Puebla, San Luis Potosí, and Chiapas (McVaugh 1983); and Nuevo León (Beetle 1983).

Vulpia myuros (L.) C.C.Gmel. (Pooideae: Poeae). Municipio de San José de Gracia, barranca Revientacuartas, Sierra San Blas de Pabellón, 2450 m, bosque de encino-pino, 12 Mar 90, *Rosales* 306 (HUAA).

Previously known in Mexico from Jalisco, Michoacán, Guanajuato, Guerrero, México, Distrito Federal, Hidalgo, Puebla, Oaxaca, and Veracruz (McVaugh 1983); Baja California Norte, Sonora, and Coahuila (Beetle 1983); Durango (Herrera 1986); and Chiapas (Valdés 1984).

ACKNOWLEDGMENTS

The authors acknowledge the reviewers for their valuable suggestions and specially to Dr. J. R. Reeder for his help in improving the English translation.

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(Received 14 July 1994; accepted 4 Nov 1994).

NOTES

TWO NEW COMBINATIONS IN *CALOCHORTUS CLAVATUS* (LILIACEAE).—Peggy L. Fiedler and Randy K. Zebell, Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132.

In preparation of the treatment of *Calochortus* for Volume II of the Flora of North America, it is necessary to provide taxonomic consistency in the infraspecific taxa of *C. clavatus* S. Watson. Two new combinations are formally made herein: *Calochortus c. var. pallidus* and *Calochortus c. var. recurvifolius*.

Calochortus clavatus was described from San Luis Obispo County, California, by Watson in 1879 (Proceedings of the American Academy XIV, 265). In 1925 Jepson described the first infraspecific segregate, *Calochortus c. var. avius* (Manual of the Flowering Plants of California, University of California Press, Berkeley, CA) from El Dorado County, California. Ownbey (A monograph of the genus *Calochortus*, Annals of the Missouri Botanical Garden 27:371–556, 1940) subsumed var. *avius* under var. *clavatus*. Ownbey also described a new entity, var. *gracilis* endemic to the San Gabriel Mountains. Hoover, who recognized sect. *Mariposa* as a genus, subsequently described two additional infraspecific taxa of *clavatus*, var. *pallida* and var. *recurvifolia*, (Leaflets of Western Botany, X(8):126, 1964). Munz (Supplement to a California Flora, University of California Press, Berkeley, CA, 1968) later recognized these latter two taxa as subspecies.

We recognize all five infraspecific taxa of *C. clavatus* and propose the following two new combinations so that all infraspecific taxa in *C. clavatus* are of equivalent nomenclatural rank.

1. *Calochortus clavatus* var. *pallidus* (Hoover) Fiedler and Zebell, comb. nov. *Mariposaclavata* var. *pallida* Hoover, Leaflets of Western Botany, X(8):126, 1964.—TYPE: UNITED STATES, California: San Luis Obispo Co: Summit of La Panza Range, Pozo-Simmler Road, 30 June 1955, *Hoover* 8362 (holotype: OBI!).
2. *Calochortus clavatus* var. *recurvifolius* (Hoover) Fiedler & Zebell, comb. nov. *Mariposaclavata* var. *recurvifolius* Hoover, Leaflets of Western Botany, X(8):126, 1964.—TYPE: UNITED STATES, California: San Luis Obispo Co: in heavy clay soil on ocean bluff, 3 km north of Arroyo de la Cruz on state Highway No. 1, 17 July 1954, *Hoover* 8349 (holotype: OBI!).

(Received 28 May 1995; revision accepted 5 Jun 1995)

THE STATUS OF *CASTILLEJA ATTENUATA* (SCROPHULARIACEAE) IN ARIZONA.—Mark Egger, Herbarium (WTU), Department of Botany, University of Washington, Seattle, Washington 98195.

Castilleja attenuata (A. Gray) Chuang & Heckard (previously known as *Orthocarpus attenuatus* A. Gray) is a widespread species of lowland valley and lower foothill grasslands of the Pacific slope of the western cordillera of North America from southern British Columbia to northern Baja California. A population, probably of an introduced origin, has become established on the lower Pacific slope of the Andes Mountains in southern Peru and northern Chile (Chuang and Heckard, Systematic Botany 17(3):417–431, 1992).

The fact that *Castilleja attenuata* occurs also in Arizona is not recorded in the literature until 1979 (Pinkava, Reeves, Lehto, and McGill, Journal of the Arizona-Nevada Academy of Science 14(2):37). No other published account of *C. attenuata*

mentions its distribution in Arizona, even though collections of this species from that state have accumulated slowly in Arizona herbaria over the last three decades. I have reviewed these specimens and summarize my findings below.

Apparently overlooked by Pinkava et al. (op. cit.), the first collection for Arizona seems to be of two stems mounted on a sheet deposited at ASC (Maricopa Co.: near Cave Creek Dam, 20 March 1962, L. Ellis 67), which also contains four stems of *Castilleja exserta* (A. A. Heller) Chuang & Heckard (previously known as *Orthocarpus purpurascens* Benth.). Apparently, the two stems of *Castilleja attenuata* were assumed by the collector to be depauperate specimens of *C. exserta*. Since that time, collections of *C. attenuata* from Arizona include the following (arranged chronologically):

Gila Co.: Pinal Mts., 3.3 mi N of Pioneer Pass Rec. Area, 26 April 1969, D. Keil 4528 (ASU);

Pima Co.: "extension of Tanque Verde Rd." (Redington Rd.), 6.8 mi E of W boundary of Coronado National Forest, 28 April 1973, Pinkava 10901, Lehto & Hensel (2 sheets, ASU);

Pima Co.: along Redington Rd., 5.4 mi E of W boundary of Coronado National Forest, 8 April 1978, T. Reeves 6688 (ARIZ, DES, ASU);

Pima Co.: along Redington Rd., 5.9 mi E of W boundary of Coronado National Forest, 8 April 1978, T. Reeves 6700 (ASU);

Pima Co.: along Redington Rd., 1.4 mi W of E boundary of Coronado National Forest, 8 April 1978, T. Reeves 6708 (ASU);

Pima Co.: along Redington Rd., 0.6 mi E of E boundary of Coronado National Forest, 8 April 1978, T. Reeves s.n. (ASU);

Maricopa Co.: 23 mi S of Shea Blvd on AZ Hwy. 87, near Sycamore Cr., 4 March 1985, M. Partch 247 (ASU);

Gila Co.: Sierra Ancha Wilderness Area, along Trail 128 in a corral, T5N, R14E, SW ¼, 5,000', 30 April 1992, Imdorf 641 (ASU, WTU).

I visited the Redington Pass area of Pima Co. on 17 April 1994 and located one fairly small population of *Castilleja attenuata*, consisting of perhaps 150 stems and extending for about 100 m along a small, seep-fed stream. From this population I collected one sheet of specimens (Pima Co.: ca. 5.8 mi E of W boundary of Coronado National Forest, along a small stream adjacent to Redington Rd., ca. 150 m below stock tank at Pecopia Spr., T13S, R17E, Sect. 21, NW ¼, 17 April 1994, M. Egger 619 (WTU). My collection is most likely from the same population as that of *T. Reeves 6700* cited above. Indeed, all the collections listed for Pima Co. are within 10 km of each other in the foothills separating the Rincon Mountains proper from the Santa Catalina Mountains. If these sites are considered as a single functional population, then *C. attenuata* is known presently from only five isolated locations in southcentral Arizona.

The plants at the location from which I made my collection are somewhat unusual for this species in that the bracts are mostly tipped with a shade of pale pink-purple, more like the color of the southcentral California endemic *Castilleja brevistyla* (Hoover) Chuang & Heckard than like typical *Castilleja attenuata*. This coloration is visible in almost all stems from the earlier Arizona collections as well. However, this color phase is not unknown in Californian *C. attenuata*, occurring usually in individual plants within a more typically colored general population. It may well be that the Arizona populations are predominately pink-purple as a result of the founder effect from the hypothetically small initial population(s) or from genetic drift in this strongly isolated outlying population cluster. Other than in bract coloration, the Arizona populations appear to be indistinguishable morphologically from those of the species found elsewhere. Furthermore, a chromosome count by T. Reeves of $n=12$ made from his collection #6700 (Pinkava et al., op. cit.) indicates that the Arizona populations are cytologically similar to those from other regions. Other published counts for *C. attenuata*, all from California collections, are of $n=12$ as well (Lewis, Madroño 15:49–52, 1959; Chuang and Heckard, Brittonia 34(1):89–101, 1982).

The origin of the Arizona populations of *Castilleja attenuata* is open to question. These populations appear to be disjunct from the main range of the species by at

least 350 km of largely inhospitable habitat. It is possible that they may be relicts from a more continuous range in the past, presumably during the Pleistocene glaciation. This scenario could account for the divergence in bract tip coloration. However, it might be suggested that the Arizona isolates should have diverged more significantly from the main species in some tens of thousands of years.

Another hypothesis is that *Castilleja attenuata* was introduced through human activity, either intentional or unintentional. It seems unlikely that this relatively nondescript and insubstantial species would have been consciously introduced. Some minor support is provided for an unintentional introduction scenario by the fact that all of the known Arizona populations are very close to roadways. The existence of the apparently introduced populations in Peru and Chile also lend some support to the likelihood of an origin by unintended human introduction for the Arizona populations.

Comments on the Conservation Status of Castilleja attenuata in Arizona. While this species is abundant in many parts of its range, its status as a component of the flora of Arizona is open to some question and concern. While it does show some evidence of an ability to colonize new areas, *C. attenuata* exhibits none of the characteristics one would associate with an invasive weed. It is strongly limited to very specific native habitats, and this appears to be especially true of the Arizona populations. The few known sites for this species in Arizona should be regularly monitored, as changes in the hydrology of the sites, development for agriculture or construction, and trampling by livestock and/or ORVs could all cause these populations to decline or to become extirpated.

I express my appreciation to C. Hamilton (WTU) for helpful comments on this note and to the curatorial staff at ARIZ, ASC, ASU and DES herbaria for the timely loan of specimens.

(Received 7 Oct 1994; accepted 30 Oct 1994)

NOTEWORTHY COLLECTIONS

ARIZONA

BERBERIS HARRISONIANA Kearny and Peebles (BERBERIDACEAE)—Maricopa Co., Sand Tank Mountains, one mile southwest of Squaw Tit, at 32°40'N, 112°24'W. About two dozen shrubs, averaging one meter tall, some in flower, in shady north-facing alcove in tertiary volcanics, along rocky drainage with *Vauquelinia californica* and *Juniperus erythrocarpa*. T9S, R1W, Sect. 6, S½, 1050 m, 2 Jan 1995, J. Malusa, ARIZ.

Significance. *Berberis harrisoniana*, the Kofa Mt. Barberry, was previously known from only two locales—the Kofa Mts. and the Ajo Mts., also in western Arizona (LaFerriere, J., Berberidaceae. Jour. of Ariz.-Nev. Acad. Sci. 26(1):2–4, 1992). Both in the Ajos and the Kofas it has been collected in only two canyons, where there is sufficient relief to provide a relatively mesic microhabitat. The surrounding land receives 5 to 10 inches of precipitation annually. The new population described here, in the Sand Tank Mts., is about 45 miles north of the Ajo Mts., and 120 southeast of the Kofa Mts. Hence, the three locales likely to have no genetic communication. Despite its highly restricted distribution, *Berberis harrisoniana* has no obvious threats,

and its Federal status is Category 3C, i.e., considered for listing, but deemed not threatened. It is protected by the absence of roads, people, and livestock.

—JAMES MALUSA, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson 85721.

CALIFORNIA

GASTROCLONIUM COMPRESSUM (Hollenb.) C. F. Chang & B. M. Xia (CHAMPIACEAE).—Marin Co., Tomales Bay, Tomales Beach. 122°82'W, 38°10'N in midtidal to lower intertidal, growing on the bottoms and the sides of 20–50 kg. rocks, with *Polysiphonia pacifica*, epiphytic on *Chondracanthus canaliculatus*, 9 Aug 1994, J. Hughey and F. Perez (NCC, UC).

Previous knowledge. The distribution of this alga is from Baja California to the Monterey Peninsula (I. A. Abbott and G. J. Hollenberg, *The Marine Algae of California*, 1976).

Significance. Extends distribution ca. 190 km N.

CENTROCERAS CLAVULATUM (C.Ag) Mont. (CERAMIACEAE).—Marin Co., Tomales Bay, Avalis Beach. 122°94'W, 38°14'N, lower intertidal, saxicolous and epiphytic on *Neorhodomela larix*, 7 Jan 1994, J. Hughey (NCC, UC); Tomales Bay, Nick's Cove. 122°82'W, 38°12'N, lower intertidal, saxicolous, with *Gratelouphia setchellii* and *Prionitis lanceolata*, 26 May 1994, J. Hughey (UC).

Previous knowledge. The northern distribution limit of this broadly distributed red alga is reported to be Santa Cruz, California (I. A. Abbott and G. J. Hollenberg, *The Marine Algae of California*, 1976).

Significance. Extends distribution ca. 160 km N. This alga was collected in a sand-swept, semi-exposed locality at Avalis Beach and in a sheltered locality at Nick's Cove. The regular, narrowly divaricate dichotomies of *Centroceras clavulatum* distinguish it in the field from species of *Ceramium*.

FUCUS SPIRALIS L. (FUCACEAE).—Marine Co., Tomales Bay, White Gulch. 122°88'W, 38°12'N, high intertidal, saxicolous and on partly buried logs, with *Pelvetiopsis limiflata*, mostly at a higher level than *Fucus gardneri* plants though partly intermixed with them, 6 Feb 1994, J. Hughey (NCC, UC).

Previous knowledge. This brown alga, which is common and abundant in the North Atlantic, was reported for the Pacific Coast for the first time twenty years ago (R. E. Norris and E. Conway, *Sysis*, 7:79–81, 1974). Norris and Conway cited specimens from the Aleutians to northern Washington. According to Silva, Deew, and Rasmussen (personal communication), the species also occurs in Humboldt Bay.

Significance. Extends distribution ca. 320 km S. *Fucus spiralis* can be distinguished from *F. gardneri* by its spiraling thallus, strongly distinct and percurrent midrib, and lack of caecostomata. In examination of 10 plants of each species, I found no caecostomata in 450 transverse sections of *F. spiralis* and 107 caecostomata in 250 transverse sections of *F. gardneri*.

—JEFFERY R. HUGHEY, Department of Biology, Sonoma State University, Rohnert Park, CA 94928.

SONORA

THERMOPSIS MONTANA Nuttall ex Torry & A. Gray var. *MONTANA* (FABACEAE).—Sonora, Sierra de los Ajos, Arroyo Frijolito, 30°57'N, 109°57'W, elev. 2075 m, east-facing slope near canyon bottom in pine-oak forest with *Abies concolor*, *Quercus*

arizonica, *Populus tremuloides*, *Fraxinus*, *Rhus*, *Senecio*, and *Malaxis ehrenbergii*, 9 Oct 1992, *Mark Fishbein* 737, *Richard S. Felger*, *Florentino Garza Salazar*, *Martín Haro Rodriguez* (ARIZ).

Previous knowledge. This variety is widespread in the intermountain region of the western United States, from Oregon southeast to New Mexico (C. J. Chen, M. G. Mendenhall, and B. L. Turner, Annals of the Missouri Botanical Garden 81:714–742, 1994). The nearest known population to the new collection occurs approximately 125 km to northeast in the Chiricahua Mountains of southeastern Arizona.

Significance. First report of this genus from México. This is the third record of a species known in México only from the Sierra de los Ajos (Madroño 40:270–271, 1993; M. Fishbein, R. S. Felger, and F. Garza Salazar in DeBano and Folliot, Proceedings of the Conference on Biological Diversity and Management of the Madrean Archipelago, USDA Forest Service General Technical Report, in press).

—MARK FISHBEIN, Herbarium and Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721 and RICHARD S. FELGER, Drylands Institute, 2509 N. Campbell #126, Tucson, AZ 85719.

ASCLEPIAS LEMMONI A. Gray (ASCLEPIADACEAE).—Near La Huerta, N side of Sierra de Alamos, ca. 4 km SW of Alamos, 26°59'15"N, 108°58'30"W, 1200 m, rare tall perennial herb in recently burned oak woodland, *V. W. Steinmann* 93-336 (27 Aug 1993, ARIZ).

Previous knowledge. Mountains of Cochise and Pima counties, Arizona, southward in the Sierra Madre Occidental to Chihuahua, Durango, Jalisco, and Sinaloa. The only previous Sonoran locality is the Sierra San Jose, just S of Naco, Cochise County, Arizona.

Significance. Second Sonoran locality and a range extension of 450 km to the south in Sonora.

CYNANCHUM WIGGINSII Shinners (ASCLEPIADACEAE).—North side of Sierra de Alamos, vic. 26°59'30"N, 108°58'W, 900 m, twining herb in oak woodland, *V. W. Steinmann* s.n. (19 Aug 1992, ARIZ, det. M. E. Fishbein); Palm Canyon, 11.1 km SE of Magdalena on road to Cucurpe, Sierra Babiso, 1100–1200 m, 30°29'N, 110°46'W, *T. R. Van Devender* s.n. (2 Oct 1976, ARIZ), *T. R. Van Devender* s.n. (16–17 Jul 1977, ARIZ), *G. Starr* 180, *T. R. Van Devender* (14 Aug 1983, ARIZ).

Previous knowledge. Type specimen collected at Santa Cruz, Sonora, near Arizona border, but most previous records in Cochise and Santa Cruz counties, Arizona. U.S. Fish and Wildlife Service Category 2 candidate species.

Specimens from Arroyo Guajaray (*H. S. Gentry* 1098) and San Bernardo (*H. S. Gentry* 1298) in the Río Mayo region reported as *Basistelma angustifolium* (Torr. & A. Gray) Bartl. (a synonym of *C. wigginsii*) were annotated to *C. arizonicum* (A. Gray) Shinners by M. E. Fishbein.

Significance. A southern range extension of 450 km. Second and third Sonoran localities.

ABUTILON PARISHII S. Wats. (MALVACEAE).—4 km NE of El Batamote, 46 km N of Hermosillo road, 29°39'30"N, 111°00'05"W, 480 m, uncommon herbaceous perennial in rocks under trees and shrubs on granitic hills with Sinaloan thornscrub, *T. R. Van Devender* 92-3, *J. F. Wiens* (26 Jan 1992, ARIZ, TEX); common on steep volcanic slope and cliff bases, Rancho Las Viboras, Cerro Colorado, ca. 7.8 km SSW of Hermosillo, 28°58'15"N, 110°59'45"W, 240 m, *T. R. Van Devender* 94-858, *C. Peñalba* (20 Nov 1994, ARIZ, ASU, SON); steep ESE rhyolitic tuff slope and on a gentle slope in Sinaloan thornscrub, Cerro del Yeso, 28°50'30"N, 110°59'30"W, 200–300 m, *J. F. Wiens* 92-607, *C. D. Bertelsen* (7 Nov 1992, ARIZ, ASU); common on gentle SSE rhyolitic slope of riparian canyon bottom, Cañon Nacapule, 4.8 km N of San

Carlos, 27°59'25"N, 111°04'15"W, 120 m, *C. D. Bertelsen* 92-121, *J. F. Wiens* (28 Sept 1992, ARIZ, SON); common on gentle rhyolitic tuff slope, on moderate SSW-W rhyolitic tuff slope, Sinaloan thornscrub, road to Microondas Las Avispas, Sierra Libre, ca. 65 km N of Guaymas, 28°29'40"N, 111°00'40"W, 595 m, *J. F. Wiens* 92-599, *C. D. Bertelsen*, and *J. F. Wiens* 92-611, *C. D. Bertelsen* (7 Nov 1992, ARIZ, ASU).

Previous knowledge. Thought to be endemic to Pima, Santa Cruz, and Yavapai counties, Arizona. U.S. Fish and Wildlife Service Category 2 candidate species.

Significance. First Sonoran Mexican localities. A southern range extension of 250 km from the nearest Arizona population in Peck Canyon, Tumacacori Mountains, Santa Cruz County.

—THOMAS K. VAN DEVENDER, Arizona-Sonora Desert Museum, 2021 N. Kinney Road, Tucson, AZ 85743; VICTOR W. STEINMANN, Herbarium, University of Arizona, Tucson, AZ 85721; JOHN F. WIENS, Arizona-Sonora Desert Museum, Tucson, AZ 85743; C. DAVID BERTELSEN, 2503 E. Blackledge, Tucson, AZ 85716.

BLECHUM PYRAMIDATUM (Lam.) Urb. (ACANTHACEAE).—Several localities on the Río Cuchujaqui: Near junction with Arroyo El Mentidero, 11 km S of Alamos, 26°55'N, 108°55'W, 260 m, locally common herbaceous perennial, tropical deciduous forest, *T. R. Van Devender* 92-212 (4 Feb 1992, ARIZ, CAS); Rancho El Conejo, 13.4 km SSW of Alamos, 26°54'00"N, 108°55'05"W, 240 m, common in shady understory, *T. R. Van Devender* 92-621 (8 May 1992, ARIZ, UCR); Güirocoba crossing, 12.3 km SSE of Alamos, 26°56'15"N, 108°53'W, 200 m, uncommon along river, *T. R. Van Devender* 514 (5 May 1992, ARIZ); Rancheria crossing, ca. 22.5 km S of Alamos, 26°51'N, 108°55'W, 200 m, locally common on bank, *T. R. Van Devender* 92-692, *S. L. Friedman* (3 Jul 1992, ARIZ, CAS); Alamos, 27°01'N, 108°50'W, 360 m, flower bed along street, *T. R. Van Devender* 94-204 (16 Mar 1994, ARIZ); dets. T. F. Daniel.

Previous knowledge. From E and S Mexico throughout Central America, West Indies, and South America; also in Guam, Formosa, and the Philippines.

Significance. First Sonoran records.

BEGONIA PALMERI S. Wats. (BEGONIACEAE).—Río Cuchujaqui, upstream of junction with Arroyo El Mentidero, 12.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, locally common in tropical deciduous forest, shady N-facing cliff, *T. R. Van Devender* 92-957, *A. C. Sanders*, *J. F. Wiens* (5 Oct 1992, ARIZ, CAS, TEX); Arroyo El Huirotal, slopes of Sierra de Alamos, 26°56'15"N, 108°57'W, 650 m, common herbaceous perennial on shady slope, tropical deciduous forest, *T. R. Van Devender* 92-1316, *E. López-S.*, *S. A. Meyer* (13 Oct 1992, ARIZ, NOLS, UCR), *S. A. Meyer* s.n. (29 Aug 1993a, ARIZ, ASU, UCR, det. K. Burt-Utley), and *T. R. Van Devender* 94-537, *S. A. Meyer*, *J. F. Wiens* (12 Sept 1992, SON); Arroyo El Cobre, Choquincachui, 26°58'43"N, 108°40'53"W, 560 m, perennial herb on shady bank, *T. R. Van Devender* 94-733, *D. A. Yetman* (23 Sept 1994, ARIZ); perennial herb on N-slope in canyon bottom, pine-oak woodland, Sierra Sahuaribo, 1–2 km NE of El Chiribo, *V. W. Steinmann* 93-265, *M. E. Fishbein*, *D. A. Yetman* (23 Aug 1993, ARIZ).

Previous knowledge. Described from *E. Palmer* 139 collected in 1886 from Hacienda San Miguel, southwestern Chihuahua.

Significance. First Sonoran records.

ACMELLA OPPOSITIFOLIA (Lamarck) R. K. Jansen var. *OPPOSITIFOLIA* (COMPOSITAE).—Río Cuchujaqui near the junction with Arroyo El Mentidero, 12.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, rare, moist shady area at edge of river, tropical deciduous forest, *T. R. Van Devender* 93-83 (10 Mar 1993, ARIZ, CAS, SD, TEX, UCR); Near junction of Arroyo Alamos and Río Cuchujaqui, 9 km SE of Alamos, 26°57'40"N, 108°52'30"W, 280 m, tropical deciduous forest, locally com-

mon, moist soil near stream, *T. R. Van Devender 93-1405*, *J. F. Wiens* (27 Nov 1993, ARIZ, ASU, SON); along Arroyo Alamos, on E edge of Alamos, 27°00'45"N, 108°55'20"W, 400 m, locally common in moist soil, *T. R. Van Devender 92-1303*, *E. López-S.* (12 Oct 1992, ARIZ, ASU, CAS, TEX); 3 km W Bacobampo, Municipio de Etchojoa, 26°59'N, 109°40'W, 5 m, *A. C. Sanders 13586* (22 Mar 1993, UCR).

Previous knowledge. Common perennial herb in wet areas throughout tropical Latin America.

Significance. First Sonoran records.

BLUMEA VISCOSA (Mill.) D'Arcy (COMPOSITAE).—Rancheria crossing, Río Cuchujaqui, 22.5 km S of Alamos, uncommon herb along river, *T. R. Van Devender 84-217* (21 Apr 1984, ARIZ, det. G. Nesom); Arroyo El Mentidero, 11.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, uncommon on shady bank just above stream, *Van Devender 92-551*, *S. A. Meyer* (6 May 1992, ARIZ, TEX, UCR); Teachibe de Masiaca, Arroyo Masiaca, Municipio de Navojoa, 26°47'10"N, 109°14'W, 75 m, solitary in moist soil at edge of stream, *T. R. Van Devender 94-366*, *R. A. López-E.*, *D. A. Yetman* (18 Apr 1994, ARIZ).

Previous knowledge. Uncommonly found in roadsides, fields, and clearings 600–900 m or less along W coast of Mexico from Sinaloa S and E to Morelos and Veracruz, S to Central America, the West Indies and Ecuador.

Significance. First Sonoran records.

ELEPHANTOPUS SPICATUS (Aubl.) Rohr. (COMPOSITAE).—El Cajón, Río Cuchujaqui, near Rancho Palo Injerto, 15.6 km E of Alamos, 27°02.8'N, 108°44'W, 400 m, in a short tree forest, *P. D. Jenkins 91-74* (12 Mar 1991, ARIZ); Güirocoba crossing, Río Cuchujaqui, 10 km ESE of Alamos, 27°56'30"N, 108°50'W, 280 m, rare herbaceous perennial near stream under *Taxodium*, *T. R. Van Devender 92-575* (5 May 1992, ARIZ, UCR); Guayabo crossing, Río Cuchujaqui, 1.8 km NE Sabinito Sur, 14 km ESE of Alamos, 27°00'N, 108°47'45"W, 340 m, abundant herb near stream, tropical deciduous forest, *T. R. Van Devender 92-235* (5 Feb 1992, ARIZ, TEX).

Previous knowledge. An herb of disturbed areas, from Sinaloa, Nayarit, Jalisco, and Michoacán, to E Mexico, the West Indies, Central America, and French Guiana.

Significance. First Sonoran localities.

EUPATORIUM ODORATUM L. (COMPOSITAE).—Arroyo El Mentidero, 11.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, solitary shrub in tropical deciduous forest, *T. R. Van Devender 93-1318*, *S. L. Friedman* (25 Nov 1993, ARIZ, ASU, CAS, SON, TEX, UCR, det. R. K. Van Devender); on road to Alamos, ca. 600 m, *L. Mankel s.n.* (ASU, B. L. Turner).

Previous knowledge. From Sinaloa, Texas, and Florida south to Nayarit, Jalisco, Colima, and Michoacán, and further south into tropical America.

Significance. First Sonoran records.

PECTIS UNIARISTATA DC. (COMPOSITAE).—Guayabo crossing, Río Cuchujaqui, 14 km ESE of Alamos, rare annual in gravel in streambed, tropical deciduous forest with *Taxodium*–*Salix* gallery forest along stream, 27°00'05"N, 108°47'08"W, 350 m, *Van Devender 91-887*, *S. A. Meyer* (23 Oct 1991, ARIZ); Las Lajitas crossing, Río Cuchujaqui, 14.3 km ESE of Alamos, 26°59'N, 108°49'W, 320 m, common annual on bluff top above river, *T. R. Van Devender 92-1327*, *S. A. Meyer* (15 Oct 1992, ARIZ, ASU, CAS, NY, TEX, UCR).

Previous knowledge. Found in Sinaloa, Nayarit, Jalisco, Michoacán, Guerrero, and Morelos.

Significance. First Sonoran collection since Nov 1933, *H. S. Gentry 762M* at Güirocoba.

CUSCUTA BOLDINGHII Urban (CONVOLVULACEAE).—Güirocoba crossing, Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56'15"N, 108°53'W, 260 m, uncommon on

Dicliptera resupinata and *Sida* sp., sandbars above river, tropical deciduous forest with *Taxodium*–*Salix* gallery forest along stream, *T. R. Van Devender* 92-31 (28 Jan 1992, ARIZ, UC), det. K. J. Johnson, ver. T. Beliz.

Previous knowledge. Yucatán, Veracruz, Michoacán, Guerrero, to the West Indies and Central America.

Significance. First Sonoran record.

CUSCUTA POTOSINA Schaffner var. *GLOBIFERA* Schaffner (CONVOLVULACEAE).—Ridge above Guayabo crossing, Río Cuchujaqui, 2.6 km NE of Sabinito Sur, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W, 370 m, common parasite on *Ayenia filiformis* and *Evolvulus alsinoides*, recently clear cut tropical deciduous forest, *V. W. Steinmann* 93-349, *S. A. Meyer*, *Van Devender* (21 Nov 1993, ARIZ, ASU, UC, UCR), det. T. Beliz.

Previous knowledge. Arizona and New Mexico. Central and S Mexico.

Significance. First Sonoran record.

IPOMOEA MEYERI (Spreng) G. Don (CONVOLVULACEAE).—Rancheria crossing, Río Cuchujaqui, ca. 22.5 km S of Alamos, 26°51'N, 108°55'W, 200 m, common annual on dense bank, tropical deciduous forest, *T. R. Van Devender* 92-1149 (10 Oct 1992, ARIZ, FAU, UCR); Güirocoba crossing, Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56'15"N, 108°53'W, 260 m, solitary in shady canyon, tropical deciduous forest, *T. R. Van Devender* 92-914, *A. C. Sanders*, *J. F. Wiens* (4 Oct 1992, ARIZ); dets. V. W. Steinmann, D. A. Austin.

Previous knowledge. Sinaloa S through most of tropical Mexico, Central and South America, the West Indies.

Significance. First Sonoran records.

MERREMIA QUINQUEFOLIA Hallier f. (CONVOLVULACEAE).—Güirocoba crossing, Río Cuchujaqui, 12.3 km SSE of Alamos, 27°56'15"N, 108°53'W, 260 m, locally common vine on dense *Perityle microglossa* near river, *T. R. Van Devender* 92-522 (5 May 1992, ARIZ, det. K. J. Johnson, ver. D. F. Austin); Presa Mocúzari (Adolpho Ruiz Cortínez) on Río Mayo, WNW of Alamos, 27°13'10"N, 109°06'30"W, 120 m, locally common, to 3 m high in shrubs, *T. R. Van Devender* 92-1391 (16 Oct 1992, ARIZ, FAU, UCR); Arroyo Guajaráy, 6.5 km WNW of junction with Río Mayo, 27°36'N, 108°55'45"W, 270 m, tropical deciduous forest, rocky stream canyon below Guajaráy, *T. R. Van Devender* 93-429 and 93-454, *V. W. Steinmann*, *D. A. Yetman* (19 Mar 1993, ASU, ARIZ, FAU, UCR).

Previous knowledge. From Culiacan, Sinaloa, and Baja California, S Florida, the West Indies, and South America.

Significance. First Sonoran records.

CYPERUS DIFFORMIS L. (CYPERACEAE).—Arroyo El Mentidero, 11.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, locally common perennial herb in shallow stream, canyon bottom, tropical deciduous forest, *T. R. Van Devender* 93-1307, *S. L. Friedman* (25 Nov 1993, ARIZ, NYSM), det. G. C. Tucker.

Previous knowledge. Scattered localities across the S United States, central Mexico, West Indies and South America. In Mexico it is known from Sonora, Sinaloa, Jalisco, Guanajuato, and Michoacán.

Significance. Only previous Sonoran record was Wright 1950 in 1851 from Santa Cruz, just north of the San Rafael Valley, Santa Cruz County, Arizona border (in 1851). Charles Wright collected in Santa Cruz County, then in Sonora, on the boundary survey prior to the Gadsden Purchase of 1853.

EUPHORBIA OCYMOIDEA L. var. *BARNESII* (Millsp.) McVaugh (EUPHORBIACEAE).—In shade near Rancho San Pedro, El Cajón, Río Cuchujaqui, 23 km E, 4 km N of Alamos, 27°02'N, 108°42'W, 450 m, *P. D. Jenkins* 89-414 (13 Mar 1989, ARIZ); Guayabo crossing, Río Cuchujaqui, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W,

350 m, rare at shady cliff base in tropical deciduous forest with *Taxodium-Salix* gallery forest along stream, *T. R. Van Devender 91-906*, *S. A. Meyer* (23 Oct 1993, ARIZ); in canyon above La Aduana, N side of Sierra de Alamos, 6 km W of Alamos, 27°01'20"N, 109°00'45"W, 850 m, rare annual in shady tropical deciduous forest understory, *T. R. Van Devender 90-622*, *S. A. Meyer* (30 Dec 1990, ARIZ), *T. R. Van Devender 92-242*, *V. W. Steinmann*, *S. L. Friedman* (5 Feb 1992, ARIZ), *T. R. Van Devender 93-1185*, *V. W. Steinmann*, *S. L. Friedman* (21 Nov 1993, ARIZ); tropical deciduous forest below Microondas La Luna, Cerro las Tatemas, 13.8 km NW of Alamos, 27°07'N, 109°02'W, 700 m, *A. C. Sanders 9462* (6 Sept 1989, ARIZ, UCR), and *P. D. Jenkins 90-277*, *P. S. Martin* (10 Oct 1990, ARIZ).

Previous knowledge. From Sinaloa, Tamaulipas, Michoacán and San Luis Potosí, to Veracruz and Guerrero, S through Central America to Panama.

Significance. First Sonoran records. Major northward range extension from Jalisco.

BOTHRIOCLOA PERTUSA (L.) A. Camus (GRAMINEAE).—Arroyo El Mentidero, 11.5 km S of Alamos, 26°54'55"N, 108°55'05"W, 240 m, disturbed roadside, tropical deciduous forest, *T. R. Van Devender 93-59* (9 Mar 1993, ARIZ), det. J. R. Reeder.

Previous knowledge. Occurring from North Africa to India and China, introduced into several United States Experimental Station sites but persisting only in S Texas.

Significance. First record for Sonora.

BOUTELOUA ALAMOSANA Vasey (GRAMINEAE).—Three localities in tropical deciduous forest along Río Cuchujaqui: junction with Arroyo Alamos, 11.3 km SE of Alamos, 26°57'30"N, 108°52'W, 280 m, uncommon on ledge above river, *T. R. Van Devender 91-751*, *S. A. Meyer* (27 Sept 1991, ARIZ); Güirocoba crossing, 12.3 km SSE of Alamos, 26°56'15"N, 108°53'W, 260 m, locally abundant on top of bluffs, *T. R. Van Devender 92-9044* (4 Oct 1992, ARIZ, ASU, CAS, SD, TEX); Guayabo crossing, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W, 350 m, locally common on top of bluffs, *T. R. Van Devender 93-1238*, *V. W. Steinmann*, *J. F. Wiens* (21 Nov 1993, ARIZ, ASU); dets. J. R. Reeder.

Previous knowledge. Mexico: Sonora, Chiapas, Oaxaca. Central America. Known from four localities in Sonora.

Significance. First collections from southern Sonora since September 1890 (the holotype: *E. Palmer 698*, near Alamos, US, NY, TAES). Considering that Palmer visited the Río Cuchujaqui in 1890 and that *B. alamosana* is restricted to depressions on volcanic benches along the river, the type specimens may well have come from the Güirocoba crossing. These localities are higher (260–350 m) than the “less than 100 m (at Alamos)” cited for the lower elevational limit for the species by Gould (1979; Ann Mo. Bot. Gard. 66:383).

DESMODIUM SCOPULORUM S. Wats. (LEGUMINOSAE).—Arroyo El Mentidero, 11.5 km S of Alamos, 26°54'55"N, 108°55'05"W, 240 m, solitary annual(?) herb in tropical deciduous forest on ledge, *T. R. Van Devender 93-848*, *D. A. Yetman*, *R. A. López-E.* (20 Sept 1993, ARIZ, NY, UCR), det. V. W Steinmann, ver. R. C. Barneby.

Previous knowledge. Previously only known from the type locality in mountains above Guaymas (*E. Palmer 258*, 1887), and 30 km N of Colorado on road to Mazatlán (*I. L. Wiggins*, *R. C. Rollins 370*, 1941).

Significance. A range extension of about 250 km to the SE.

DESMODIUM SCORPIURUS (Sw.) Desv. (LEGUMINOSAE).—Several localities for this herbaceous perennial in sand under *Taxodium mucronatum* in riparian gallery forests along the Río Cuchujaqui, tropical deciduous forest on slopes: Güirocoba crossing, 12.5 km SSE of Alamos, 26°56'15"N, 108°53'W, 260 m, *A. C. Sanders 3684* (25 Mar 1983, NY, UCR); Rancho El Conejo, 12.4 km S of Alamos, 26°54'35"N, 108°55'W, 240 m, very common near stream, *T. R. Van Devender 92-582*, *S. A. Meyer* (7 May 1992, ARIZ), *T. R. Van Devender 92-637* (8 May 1992, ARIZ, UCR); Rancheria

crossing, ca. 22.5 km S of Alamos, 26°51'N, 108°55'W, 200 m, *T. R. Van Devender* 92-1154, *A. C. Sanders* (10 Oct 1992, ARIZ); Guayabo crossing, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W, 350 m, uncommon along edge of disturbed road, *T. R. Van Devender* 92-1255, *E. López-S.* (12 Oct 1992, ARIZ, ASU, CAS, SON), *T. R. Van Devender* 93-200, *S. L. Friedman* (12 Mar 1993, ARIZ, ASU), *T. R. Van Devender* 94-291 (14 Apr 1994, ARIZ, SON); near Arroyo El Mentidero junction, 12.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, uncommon, twining at the base of *Hymenoclea* at edge of river, *T. R. Van Devender* 93-92 (10 Mar 1993, ARIZ). Frijol de codorniz (Spanish), suvaqui muni (Mayo).

Previous knowledge. From Sinaloa S to Central America, West Indies, and South America. Old World tropics, where introduced, or Taiwan and the Philippines, perhaps native.

Significance. First Sonoran records.

MIMOSA DIPLOTRICHA C. Wright var. *ODIBILIS* Barneby (LEGUMINOSAE).—Guayabo crossing, Río Cuchujaqui, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W, 350 m, solitary annual in sand in streambed in *Taxodium*-*Salix* gallery forest, *T. R. Van Devender* 92-1284, *E. López-S.* (12 Oct 1992, ARIZ), det. R. C. Barneby.

Previous knowledge. A rare annual known from Chihuahua, Sinaloa, and Michoacán, and of considerably lower elevation than *H. S. Gentry* 2635, from 915 m at Cienegita, Chihuahua—the type of *Schrankia heterocarpa* Standl., a synonym.

Significance. First Sonoran record.

PHASEOLUS LUNATUS L. (LEGUMINOSAE).—Arroyo El Mentidero, 11.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, solitary annual vine on *Senna pallida* in tropical deciduous forest, *T. R. Van Devender* 92-537, *S. A. Meyer* (6 May 1992, ARIZ, UCR) and *T. R. Van Devender* 94-184 (16 Mar 1994, ARIZ, ASU, NY, SON, UCR); below Guajaráy, Arroyo Guajaráy, 6.5 km (by air) WNW of junction with Río Mayo, 27°36'N, 108°55'45"W, 270 m, very common in tropical deciduous forest in rocky stream canyon, *T. R. Van Devender* 93-468, *V. W. Steinmann*, *D. A. Yetman* (19 Mar 1993, ARIZ, NY, SON).

Previous knowledge. Much of lowland tropical America, from Sinaloa, Nayarit, Jalisco, and Tamaulipas, south to Veracruz, Oaxaca, Central America, the West Indies, and South America.

Significance. First records for Sonora.

POLYPREMUM PROCUMBENS L. (LOGANIACEAE).—Arroyo El Mentidero, just above junction with Río Cuchujaqui, 11 km S of Alamos, 26°55'N, 108°55'W, 260 m, common along stream, *T. R. Van Devender* 92-180 (4 Feb 1992, ARIZ), *T. R. Van Devender* 92-949, *S. A. Meyer*, *A. C. Sanders* (4 Oct 1994, ARIZ, ASU, CAS, MO, SD, TEX, UCR), and *T. R. Van Devender* 93-1314, *S. L. Friedman* (25 Nov 1993, NY), det. P. D. Jenkins.

Previous knowledge. From SE U.S. and Mexico to the West Indies, Central America, and N South America

Significance. First Sonoran locality.

PASSIFLORA SUBEROSA L. (PASSIFLORACEAE).—Arroyo El Mentidero, 11.5 km S of Alamos, 26°54'55"N, 108°55'05"W, 240 m, solitary perennial vine in *Haematoxylon*, *T. R. Van Devender* 93-66 (10 Mar 1993, ARIZ, MO, UCR); Guayabo crossing, Río Cuchujaqui, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W, 350 m, rare in crack in ledge above river with *Taxodium*-*Salix* gallery forest along stream, tropical deciduous forest on slopes, *T. R. Van Devender* 93-1200 (21 Nov 1993, ARIZ); near Tojibampo, 19.5 km N of San Bernardo on the road to Mesa Colorada, 27°01'45"N, 108°46'45"W, 740 m, solitary in rocky canyon bottom, tropical deciduous forest, *T. R. Van Devender* 93-1500A, *R. A. López-E.*, *D. A. Yetman* (11 Dec 1993, ARIZ, ASDM [live], MO); dets. J. M. MacDougal.

Previous knowledge. From Florida, southernmost Texas, and the West Indies to Argentina. In Mexico, generally S and E of Guadalajara, with one photo record from Nayarit (J. M. MacDougal personal communication, 1993).

Significance. First Sonoran records.

PIPER JALISCANUM S. Wats. (PIPERACEAE).—Sierra de Alamos, 850 m, rare in shady rocky tropical deciduous forest canyon above La Aduana, *P. D. Jenkins* 89-444, *S. A. Meyer*, *P. Todd* (24 Dec 1989, ARIZ), *P. D. Jenkins* 90-248 (8 Oct 1990, ARIZ), and *T. R. Van Devender* 90-635, *S. A. Meyer* (30 Dec 1990, ARIZ, det. *P. D. Jenkins*); Guayabo crossing, Río Cuchujaqui, 27°00'05"N, 108°47'08"W, 350 m, solitary on rock in shady understory of tropical deciduous forest, *T. R. Van Devender* 93-1178 (21 Nov 1993, ARIZ); Güirocoba crossing, Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56'15"N, 108°53'W, 260 m, solitary shrub in shady canyon in tropical deciduous forest, *T. R. Van Devender* 94-182 (11 Mar 1994, ARIZ).

Previous knowledge. Sinaloa, Nayarit, and Jalisco.

Significance. First Sonoran records.

CRUEA CORONATA Rob & Greenm. (RUBIACEAE).—Rancheria crossing, Río Cuchujaqui, 22.5 km S of Alamos, 26°51'N, 108°55'W, 200 m, rare annual in sandy, rocky river bottom, tropical deciduous forest, *T. R. Van Devender* 92-1189, *A. C. Sanders* (10 Oct 1992, ARIZ).

Previous knowledge. A rare plant known from Sinaloa, Jalisco, Guerrero, and Mexico.

Significance. First record for Sonora.

CRUEA PSYLLIOIDES (H.B.K.) W. R. Anderson (RUBIACEAE).—Arroyo El Mentero, 11.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, rare annual in arroyo bottom, tropical deciduous forest, *T. R. Van Devender* 92-965 (5 Oct 1992, ARIZ); Rancho las Uvalamas, E side of Sierra de Alamos, S of Alamos, *S. A. Meyer s.n.* (2 Oct 1992, ARIZ).

Previous knowledge. Lower mountain slopes from S Sonora and Chihuahua to W Chiapas.

Significance. First Sonoran collections since 1933 (*H. S. Gentry* 428MG, Cañon Estrella, vic. Alamos).

DIODIA SARMENTOSA Sw. (RUBIACEAE).—Various localities in bottoms of stream canyons with tropical deciduous forest on slopes: Guayabo crossing, Río Cuchujaqui, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W, 350 m, *A. C. Sanders* 9399 (6 Sept 1989, UCR); upstream of Las Lajitas crossing, Río Cuchujaqui, 5.6 km ESE of Alamos, 26°59'N, 108°49'W, 320 m, *T. R. Van Devender* 92-786a, *S. A. Meyer*, *S. L. Friedman* (7 Jul 1992); Río Cuchujaqui at Rancho El Conejo, 13.4 km S of Alamos, 26°54'N, 108°55'W, 220 m, *T. R. Van Devender* 92-632 (8 May 1992, ARIZ, UCR, det. *K. J. Johnson*); Parque Chalaton, NE side of Sierra de Alamos, 27°00'55"N, 108°56'35"W, 420 m, *A. C. Sanders* 13268 (16 Mar 1993, UCR); Arroyo El Huirotal, E slopes of Sierra de Alamos, 11 km SSW of Alamos, 26°55'N, 108°55'W, 600 m, sprawling in streambed, tropical deciduous forest, *T. R. Van Devender* 90-657, *S. A. Meyer* (31 Dec 1990, ARIZ) and *T. R. Van Devender* 92-67 (30 Jan 1992, ARIZ, TEX, UCR); Rancho la Sierrita, E slopes of Sierra de Alamos, ca. 6 km SSW of Alamos, 26°58'30"N, 108°58'05"W, 925 m, *Martin s.n.* (27 Aug 1990, ARIZ, det. *V. W. Steinmann*); Arroyo Guajaráy, between Rancho La Junta on the Río Mayo and Guajaráy, 27°35'15"-27°36'N, 108°52'-108°55'45"W, 240 m, uncommon, *T. R. Van Devender* 93-414, *V. W. Steinmann*, *D. A. Yetman* (18 Mar 1993, ARIZ); uncommon in Arroyo El Cobre, Choquinahui, 26°58'48"N, 108°40'53"W, 560 m, *T. R. Van Devender* 94-720, *D. A. Yetman* (23 Sept 1994, ARIZ).

Previous knowledge. From S Mexico, and Guatemala, S and E to Panama, Guianas, and the West Indies.

Significance. First records for Sonora.

HEDYOTIS VEGRANDIS W. H. Lewis (Rubiaceae).—Güirocoba crossing of Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56'15"N, 108°53'W, 260 m, rare annual on exposed bench above river, tropical deciduous forest, *V. W. Steinmann s.n.*, *C. M. Smith* (21 Aug 1992, ARIZ).

Previous knowledge. Baja California, Sonora, and Sinaloa.

Significance. First Sonoran locality since *I. L. Wiggins & R. C. Rollins 135* (1941), 16.9 km W of Hermosillo on road to Kino Bay.

ANEMIA AFFINIS Baker in Hook & Baker (Schizaeaceae).—Guayabo crossing, Río Cuchujaqui, 14 km ESE of Alamos, 27°00'05"N, 108°47'08"W, 350 m, locally common, on mossy boulder on shady bank near river in *Taxodium-Salix* gallery forest, tropical deciduous forest on slopes, *T. R. Van Devender 93-1169*, *V. W. Steinmann*, *S. L. Friedman* (21 Nov 1993, ARIZ, ASU, MO, UCR, det. G. Yatskievych); Arroyo Santa Barbara, Municipio de Alamos, 27°05.4'N, 108°43.3'W, 1000 m, in shady rocks along trail by stream, topical deciduous forest, *P. D. Jenkins 90-191* (6 Oct 1990, ARIZ); Ranch Agua Blanca, 28°59'00"N, 109°05'20"W, 1000–1100 m, on basaltic soils in Chihuahua oak woodland, *P. S. Martin s.n.* (6 Nov 1986, ARIZ); on broken volcanic rocks under oaks on slopes, oak woodland, 915–1067 m, *H. S. Gentry 19338* (16–18 Oct 1961, ARIZ).

Previous knowledge. In the Sierra Madre of Sonora, Sinaloa, Nayarit, and Jalisco.

Significance. First Sonoran localities with data.

NICOTIANA PLUMBAGINIFOLIA Viviani (Solanaceae).—Río Cuchujaqui near junction with Arroyo El Mentidero, 12.3 km S of Alamos, 26°54'45"N, 108°55'05"W, 240 m, moist sand, *T. R. Van Devender 92-682*, *S. L. Friedman* (2 Jul 1992, ARIZ, UCR); Rancheria crossing, Río Cuchujaqui, ca. 22.5 km S of Alamos, 26°51'N, 108°55'W, 200 m, moist soil at edge of stream, *T. R. Van Devender 92-700A*, *S. L. Friedman* (3 Jul 1992, observ.); upstream of Las Lajitas crossing, Río Cuchujaqui, 5.6 km S of Alamos, 26°59'N, 108°59'W, 320 m, moist soil near stream, *T. R. Van Devender 92-799A*, *S. L. Friedman*, *S. A. Meyer* (7 Jul 1992, observ.); Güirocoba crossing, Río Cuchujaqui, dry streambed, *T. R. Van Devender 84-169* (20 Apr 1984, ARIZ); Arroyo El Huirotal, E slopes of Sierra de Alamos, 7 km SW of Alamos, 26°56'15"N, 108°57'W, 550 m, shady rocky streambed in tropical deciduous forest, *T. R. Van Devender 92-757* (6 Jul 1992, ARIZ).

Previous knowledge. Wet sandy areas and in waste areas, from the Florida Keys, West Indies, Mexico, and Guatemala to South America.

Significance. First Sonoran records since 1948 (*H. S. Gentry 7941*, near Navojoa).

PHYLLOSTRIGULOSA (Mart. & Gal.) Moldenke (Verbenaceae).—Rancheria crossing, Río Cuchujaqui, ca. 22.5 km S of Alamos, 26°51'N, 108°55'W, 200 m, single dense patch in the shade of shrubs on river bank, *T. R. Van Devender 92-710*, *S. L. Friedman* (3 Jul 1992, ARIZ), det. A. D. Harlan.

Previous knowledge. Widespread from Rio Grande Valley of Texas, south to Central and South America, and the West Indies.

Significance. First Sonoran record. Nearest locality believed to be Culiacan, Sinaloa, 250 km to the south.

—THOMAS K. VAN DEVENDER, Arizona-Sonora Desert Museum, 2021 N. Kinney Road, Tucson, AZ 85743; ANDREW C. SANDERS, Herbarium, University of California, Riverside, CA 92521; VICTOR W. STEINMANN, Herbarium, University of Arizona, Tucson, AZ 85721; REBECCA K. VAN DEVENDER, Herbarium, University of Arizona,

Tucson, AZ 85721; STEPHANIE A. MEYER, Apartado Postal 34, Alamos 85760, Sonora; SAMUEL L. FRIEDMAN, Herbarium, Arizona State University, Tempe, AZ 85281; JOHN F. WIENS, Arizona-Sonora Desert Museum, Tucson, AZ 85743; DAVID A. YETMAN, Southwest Center, University of Arizona, Tucson, AZ 85721; PHILIP D. JENKINS, Herbarium, University of Arizona, Tucson, AZ 85721; EDUARDO LOPEZ-SAAVEDRA, Centro Ecológico de Sonora, A.P. 1497, Hermosillo 83000, Sonora; RIGOBERTO A. LOPEZ-ESTUDILLO, Centro de Investigaciones Científicas y Tecnológicas de la Universidad de Sonora, Hermosillo 83000, Sonora; JAMES D. FREEH, Herbarium, University of Arizona, Tucson, AZ 85721.

ANNOUNCEMENT

A CALIFORNIA FLORA DATABASE NOW AVAILABLE

A database on California plant distributions is now available from the US Forest Service, Pacific Southwest Research Station. The California Flora Database contains nomenclature, geographic and ecological information for 6717 California vascular plant taxa, as well as additional habitat information for rare taxa and species of the Sierra Nevada. Each species-level taxon listed in A California Flora and Supplement (Munz and Keck 1968) is referenced in the database, plus additional records for infraspecific taxa listed in the CNPS Inventory of Rare and Endangered Vascular Plants of California (Skinner and Pavlik 1994).

The database is useful as a first step in developing local species and rare plant checklists, for creating broad overviews of species distributions, and for floristic analyses. The California Flora Database is useful to community groups, planning agencies, state and local agencies, consulting firms, and researchers.

The database is provided as a 2.2 mg ASCII file designed for easy import into the user's database software. The file is available for anonymous ftp at: s27w007.pswfs.gov/pub/ifg/calflora.txt

Corrections and additions are made periodically. Questions and comments can be addressed to:

Ann Dennis, Ph.D.
USDA FS, PSW
P.O. Box 245
Berkeley, CA 94701
email: ad@s27w007.pswfs.gov

OBITUARY

KITTIE FENLEY PARKER (1910–1994)

Dr. Kittie Fenley Parker died on 9 November 1994 in San Diego, CA, USA. She was a Professor Emeritus of Botany at George Washington University (GWU) and a Research Associate of the Smithsonian Institution, both Washington, DC, USA. She received a BA (1930) and an MA (1932) from the University of California at Berkeley and PhD (1946) from the University of Arizona. She began teaching botany courses first in the School of Agriculture at the University of Arizona and later in the 1950's at George Washington University where she rose to the rank of Full Professor. At GWU she taught popular undergraduate courses in field botany, taxonomy of flowering plants, horticulture, economic botany, and graduate courses in plant systematics, including systematics of Poaceae and Asteraceae. She retired from GWU in 1979, received emeritus status, and continued to teach horticulture for several more years. The new greenhouse at GWU was named for her as a tribute to the plant teaching-collection she accumulated and maintained.

Between 1959 and 1989, Kittie also worked in her spare time in the Department of Botany, Smithsonian Institution. Here she identified hundreds of Mexican Asteraceae collections that had been sent to the U.S. National Herbarium for identification and pursued her research interest in *Hymenoxys* and *Tetraneuris* (both Asteraceae). She published her research on the South American species of both genera. While at the Smithsonian, Kittie was very instrumental in placing a number of her botany students in various open positions in the Department of Botany.

She was also an active member and past president of the Botanical Society of Washington and a long-time member and former secretary of the Potomac Chrysanthemum Society. Her late husband, Kenneth Parker, was Chief of the Range Research Division of the U.S. Forest Service. Kittie is survived by two grand-daughters. She will long be remembered by her many friends and colleagues in the Department of Botany for her kindness and outgoing personality.

—DIETER C. WASSHAUSEN, Department of Botany, NHB-166, Smithsonian Institution, Washington, D.C. 20560-0001, USA.

REVIEWS

Editor's Note: These two books appeared in press about the same time, and they quickly caught the eyes of the students in the Plant Taxonomy class at San Francisco State University. It was too late to have our bookstore order them for the class. I was therefore impressed when a fair number of students went out and ordered these books on their own, in addition to the required books for the course. Accordingly, the following reviews are a consensus and are based on our using them this spring.

Plants of the San Francisco Bay Region. Mendocino to Monterey. By EUGENE N. KOZLOFF and LINDA BEIDLEMAN. 1994. Sagen Press, Pacific Grove, CA. 332 pages plus 110 plates. Softcover \$35.00. ISBN 0-9643756-0-5.

The enormous diversity of plants in the California flora makes the task of identifying species daunting to many. Despite the value of such inclusive works as *The Jepson Manual of California Plants*, *Munz' Flora of California*, and *Abrams' Illustrated Flora of the Pacific Northwest*, users are often frustrated by having to wade through pages of keys and descriptions before being able to make an identification. On the other hand, local floras, dealing only with plant species of more restricted regions, are logical solutions to the needs of persons wishing to identify plants from smaller areas. Local floras are not new to California—many have been published and have served the botanical community and lay audience for over 100 years. The most recent volume, composed by Eugene Kozloff and Linda Beidleman, focuses on the San Francisco Bay region, an area having one of the higher concentrations of botanists in the country.

The book begins with a six-page introduction to such botanical basics as plant names, major plant groups, how to use a dichotomous key, conservation, and growing native plants. Following, there is a short chapter on the plant communities of the region. Most of the book consists of keys to the plant species of the Bay Area. The keys are not simply extracts of previously written keys, but rather are assembled to make identification of the Bay Area species as easy as possible. They appear to work well. The keys also follow the example of the Jepson Manual in having leads parallel in construction—a big plus.

There is an selection of high quality photographs representing a fair number of natives. Curiously, they are placed following page 74, near to but not in front of the keys. Perusing photos of Polemoniaceae we noticed several 4- and 6-merous flowers in the photos. Those who study this family know that rare deviations in merosity are not uncommon; however, *Collomia grandiflora* (plate 41) looks a bit like a member of the Rubiaceae in the photo. A bit of discussion explaining the not uncommon deviation from expected flower part number would have been helpful here. Following the photos is a section of generally good quality line drawings. Not every species in the book is illustrated, but the careful user will be able to combine the keys and illustrations to help identify plants.

Our complaints are few, and can be divided into matters technical and matters philosophical. As to the former, what strikes the reader right off is the extremely light type face used throughout the book. It appears as if the final copy was typed on a typewriter in dire need of a new ribbon. This is probably the most distracting aspect of the book. Another concern is the weight of the book—it's heavier than you'd expect. The pages are glossy and heavy weight. And the binding looks suspiciously unfieldworthy, although time will tell whether this is a real concern. Hopefully, next editions will have a typeface that matches the quality of the photographs and drawings.

As to matters of nomenclatural philosophy, we have a problem with forcing com-

mon names on species, either by translating the Latin name into English (e.g., Variedleaf Collomia for *Collomia heterophylla*) or imposing common names on species based on who knows what criterion (e.g., Common Linanthus for *Linanthus parviflorus*). Further, the practice of trying to use common names can be confusing, as when we read that the common name for *Allophylum divaricatum* is "Straggling Gilia." Keyers have enough trouble distinguishing *Allophylum* from *Gilia* without common names adding to the problem. We suggest using only those common names that are unambiguous and in *very* common use.

Overall the effort merits applause. It is a well-needed augment to the new-ish Jepson Manual, and we would advise anyone interested in the plants of the Bay Area to get a copy. Its price is reasonable, and Sagen Press will sell it directly by mail. We would like to see similar efforts written for other regions in the state for which there is no local flora.

Guide to Flowering Plant Families. By WENDY B. ZOMLEFER. 1994. The University of North Carolina Press, Chapel Hill. 430 pages. Softcover \$29.95. ISBN 0-8078-4470-5.

This is a book for which plant taxonomy students and professors have been waiting. Wendy Zomlefer has produced a text that describes major flowering plant families encountered in North America, illustrates the families in detail, and on occasion discusses problematical groups and their recent systematic treatments. She follows the system of angiosperm classification delineated by Robert Thorne, whose family circumscriptions sometimes differ a bit from those of other authors (e.g., Araliaceae are included in the Apiaceae, Asclepiadaceae are included in the Apocynaceae, *Samucus* and *Viburnum* are placed in the Adoxaceae).

The book treats in detail 115 families. Each begins with a diagnosis that stresses the features of the North American species. Following the diagnosis is a "Family Characterization" that summarizes family features, including chemical and anatomical characters. This is followed by the number of genera and species in the family, a distributional range statement, a list of major genera and U.S./Canadian representatives. Economically important members of the family are also mentioned. Each treatment ends with a commentary on the family that may deal with topics such as reproductive and pollination biology, taxonomic treatments within the family, or structures peculiar to the family. Short bibliographies that follow each family are recent.

Zomlefer includes a lucid discussion of phylogenetic systematics (=cladistics), but rather than providing a simple (or simplified) lesson that fails to convince the reader of the advantages of a cladistic approach to taxonomy, she provides a discussion of the "monocot vs dicot dilemma" from a cladistic perspective. She takes evidence from recent research that suggests that the dicots may not be monophyletic, and uses this paradigm to teach the fundamentals of phylogenetic systematics. The result is a concise, non-threatening, readable presentation of the topic that all botanists should read.

It's hard to imagine a book where a chapter on principles of cladistics is followed by one on observing, dissecting, and drawing flowering plants—but here it is. Zomlefer does not simply grace the reader with her drawing talent—she explains how to see plants and how to draw them. Zomlefer is an accomplished technical illustrator, and her drawings of the families in the book help illustrate important features. While the line drawings are not as showy as the colored figures in Heywood's *Flowering Plants of the World*, their precision will likely render them of greater use to readers.

Botanists who are interested in the latest taxonomic research, particularly in phylogenetic relationships among families, will appreciate Zomlefer's careful, articulate discussions of problematical family relationships. For example, her treatment of the

Lamiaceae and Verbenaceae includes 1) a table comparing the two families as they are circumscribed in the book, and 2) a branching diagram illustrating the relative positions of groups of Mints and Verbs. This explanatory approach allows the reader to understand the reasoning behind statements of relationship, rather than having to accept the dogma of relationships that exists in many taxonomic texts.

There is a richly illustrated glossary at the end of the book, along with one appendix that covers Cronquist's scheme of family relationships, and a chart summarizing the characteristics of the families covered in the book. The latter will be especially appreciated by students.

The only problem we had with the book is based on our western North American perspective. We are dismayed that the Hydrophyllaceae, Garryaceae, Fouquieriaceae, and Limnanthaceae were not included. We were also disappointed that the "little aquatic monocots" (e.g., Potamogetonaceae, Zanichelliaceae, Zosteraceae, Hydrocharitaceae, Juncaginaceae) were left out—all the more disappointing because Zomlefer's drawings of these families would be a great aid to those of us who are not aquatically-minded. We hereby make a plea here for future editions to include families that are important in the west, even if they aren't well-represented in the east.

A plant taxonomy course where family relationships are a component is sure to benefit from Zomlefer's book. It does more than list characters—it stimulates interest. The book will also serve professional and lay botanists as a reference on family characteristics and relationships. To be sure, as systematic research continues to resolve relationships among families, parts of this book will become dated. Nevertheless, Zomlefer has provided a first step toward a modern text in plant taxonomy. Finally, it is inexpensive, a bargain at less than \$30.

—ROBERT PATTERSON AND THE STUDENTS IN THE 1995 PLANT TAXONOMY CLASS,
Department of Biology, San Francisco State University, San Francisco, CA 94132.

Revision of the Genus Sambucus. Dissertation Botanicae, vol. 223, pp. [i–ii], 1–227–[256]. By RICHARD BOLLI. 1994. From E. Schweizerbart'sche Verlagsbuchhandlung, Johannesstrasse 3A, D-70176 Stuttgart 1, Germany. Softcover US\$45.51. ISBN 3-443-64135-0.

This new worldwide monograph (the work is much more than a mere "revision") on *Sambucus* uses morphology, anatomy, ecology, karyology, and biochemistry to recognize nine species (*S. ebulus* with 2 subspp.; *S. wightiana*; *S. adnata*; *S. gaudichaudiana*; *S. australasica*; *S. javanica*; *S. nigra* with 6 subspp.; *S. australis*; *S. racemosa* with 2 var.), eight subspecies, and two varieties. Bolli reduces some commonly accepted species to subspecies or varieties. For instance, relevant to *The Jepson Manual's* (1993) treatment of Californian taxa of *Sambucus*, according to Bolli *S. melanocarpa* becomes *S. racemosa* var. *melanocarpa*, *S. mexicana* becomes *S. nigra* subsp. *canadensis*, and *S. racemosa* var. *microbotrys* (this is not in Bolli's synonymy) and var. *racemosa* become *S. racemosa* var. *racemosa*. Bolli's two evolutionary scenarios both postulate "herbaceous *Sambucus* . . . , probably having evolved in Central Asia, . . . to represent the ancestral group" leading "independently" to "the woody taxa of both the Far East and the Western Hemisphere." *Viburnum* and *Adoxa* seem most closely related, but Bolli favors Sambucaceae excluded from Caprifoliaceae and Dipsacales. This important dissertation done at Zürich should not be overlooked due to the rather low circulation of *Dissertationes Botanicae*.

—RUDOLF SCHMID, Department of Integrative Biology, University of California, Berkeley, California 94720-3140.

LETTER TO THE EDITOR

Dear Dr. Patterson:

You usually encourage publication of work in important areas of California botany. In *Madroño* volume 42, number 1, January–March 1995, however, I felt that Peggy L. Fiedler's review of *Ethnobotany of the California Indians, Volumes 1 and 2*, by B. M. Beck and S. S. Strike, on pages 88 and 89, was not encouraging to either writers or publishers in botany.

Dr. Fielder criticizes "a lack of consistency in the listing of plant names and the inaccuracies of the index." While I grant there are inaccuracies in the index, the "lack of consistency" of plant names is quite the correct approach since Bea Beck is a librarian presenting her selection of printed work; she is not examining and correcting herbarium specimens, so she would not change names from what is given in the literature. Nomenclatural changes must be made by botanists, not by librarians.

Further, although California is fortunate to have the new *Jepson Manual*, it is not error free, and does have omissions (also true of *Ethnobotany of the California Indians*). The reviewer complains that *Scirpus lacustris* L. doesn't appear in *Jepson*. I would like to point out that *S. lacustris* L. does appear in J. C. Willis' *A Dictionary of the Flowering Plants and Ferns*, Eighth Edition, 1973 on page 1047. That work is in most libraries.

When the reviewer makes the comment "I suspect the average user . . . will not have the necessary botanical references to solve the mystery" I am amazed. All residents of California have excellent library resources and botanical references available to them.

Madroño does a good job of publishing and encouraging writers in the literature of botany. The review of this work, however, was quite unfair in her criticism of the two volume *Ethnobotany of the California Indians*. I hope your readers will ignore her review and use the books as they were intended to be used—making additions and revisions as they work.

Sincerely,
Jane B. Cole
1994–95 President, Council on Botanical and Horticultural Libraries

ANNOUNCEMENT

DESERT BOTANICAL GARDEN TO EXPAND RICHTER LIBRARY STACK SPACE BY 80 PERCENT WITH SUPPORT FROM IMS

PHOENIX—The Desert Botanical Garden's Richter Library book stack space will be increased by 80 percent due to a \$53,111 Garden project with support from the Institute of Museum Services (IMS), according to the Garden's development director, Sherry New.

The IMS-funded portion of the project totaled \$25,526 and will be used to fund environmental improvements to the library. IMS is a federal agency that offers conservation project support to the nation's museums.

Phase I of the library collection conservation plan involves the installation of six mobile track compact shelves in the library reading room to better conserve, accommodate and make library reference materials more accessible.

Phase II will perform a conservation assessment of the library collection, prioritization of materials to be treated and staff training on conservation techniques and strategies. The final library phase will be the actual conservation treatment of old, fragile and valuable materials in the collection.

This special library collection includes 10,000 volumes, many of them one of a kind, including an extensive rare book and botanical art collection. Richter Library supports research of the Garden's living and herbarium collections and is used by Garden staff and consultants as a source for information on the evolution/natural history of desert plants, ethnobotanical documentation and ecological systems of desert plant communities.

The current IMS grant makes possible the implementation of the third project of a long-range general conservation plan developed by the Desert Botanical Garden in 1989. Conservation of the living plant collection was addressed in a conservation project in 1990–1991 and conservation of the herbarium collection was implemented in a conservation project in 1992–1993. All three projects have been partially funded by grants from the Institute of Museum Services.

The Richter Library reading room receives about 4000 of the Garden's 220,000 yearly visitors and handles an additional 9000 requests for information by telephone and mail.

The Desert Botanical Garden library conservation project is partially funded by the grant from the IMS. Additional support is provided by Garden donors and members, corporate gifts and memorials.

The Desert Botanical Garden, including Richter Library, is located in Papago Park in Phoenix, Arizona. The 145-acre outdoor museum is home to 20,000 living plants representing more than 4000 different species.

ANNOUNCEMENT

LUPIN SCIENTISTS TO CONVENE AT ASILOMAR CONFERENCE CENTER IN CALIFORNIA

Scientists from throughout the world will be gathering May 11–16, 1996 for the 8th International Lupin Conference in the scenic Asilomar Conference Center near Monterey.

Lupin is grown in many counties throughout the world. Although acreage is currently small, it has the potential to become more extensively cultivated as an important protein crop. In Australia, for instance, lupin cultivation grew from zero to 1.4 million hectares (about 3.5 million acres) in just the last 20 years.

The scientists convening at Asilomar in 1996 will report on a number of topics that will be of interest to scientists and growers alike—new crop development, human and animal food uses, nitrogen fixation, ecological importance, as well as the agronomic aspects of lupin. (Note to American editors: the international scientific community spells this crop “lupin,” not “lupine.”)

A full agenda is planned for the conference, with three days of symposia scheduled in the mornings. Afternoons will be devoted to concurrent contributed papers and poster sessions in one of the following categories: agronomy, genetics, alkaloid chemistry, ecology, and utilization of lupin.

A field trip is scheduled for Tuesday, May 14, and will include visits to field plots that demonstrate the diversity of lupin and other crops grown in California. These plots are located in the Central Valley of California, one of the richest agricultural areas in the world.

“California is an important gene center for native species of lupin,” said Barbara Bentley, professor of Ecology at the State University of New York at Stony Brook. Bentley is also president of the International Lupin Association. “Of the 190 species of lupin worldwide, 120 occur in California. This conference is an exciting opportunity to foster cross-disciplinary discussion on the prospects for lupin as a crop, as well as its role in natural systems.”

Asilomar is a rustic conference center located in the dunes near the historic city of Monterey, about 100 miles south of San Francisco. The buildings are clustered among trees and native vegetation of coastal California, including at least three species of native lupin. Recreational activities include swimming, volleyball and beach combing along the spectacular California coast.

Travel to Asilomar is possible through the international airports at either San Francisco or San Jose. Scheduled air shuttle service to the Monterey airport is available from either airport. Ground transportation from the Monterey airport to Asilomar can be easily arranged.

The registration fee is \$250 if received by April 10, 1996. Housing at Asilomar starts at \$48 per day, depending on the level of luxury and number of occupants per room. The housing fee includes all standard meals at Asilomar.

This conference is being organized by the International Lupin Association and is co-sponsored by the Department of Agronomy and Range Science at the University of California, Davis and the North American Lupin Association. The ILA was founded in 1980 and meets every three years in a different country. This is the first time the conference has been held in the United States.

For further information or registration materials, write to Conference & Event Services (lupin), University of California, Davis, CA 95616-8766, USA or contact by phone at (916) 757-3331, FAX at (916) 757-7943 or by e-mail at jcbarney@ucdavis.edu. Please provide full name and address with appropriate postal codes, phone numbers, country and city codes and e-mail addresses.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$50). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

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Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used by Sivinski, Robert C., in *Madroño* 41(4), 1994. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to Brummitt and Powell, *Authors of Plant Names* (1992) and, if not included in this index, spelled out in full. Titles of all periodicals, serials, and books should be given in full. Books should include the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

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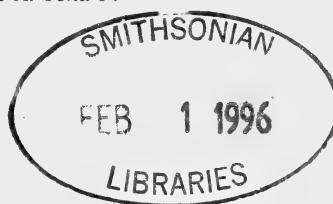
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MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$50 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to the treasurer.

Editor—ROBERT PATTERSON
Department of Biology
San Francisco State University
San Francisco, CA 94132

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ALLOZYME VARIATION IN THE AMPHITROPICAL DISJUNCT *CHABOISSAEA* (POACEAE: ERAGROSTIDEAE)

PAUL M. PETERSON

Department of Botany, National Museum of Natural History,
Smithsonian Institution, Washington, DC 20560

YOLANDA HERRERA A.

Centro Interdisciplinario de Investigacion para el
Desarrollo Integral Regional (CIIDIR),
Unidad Durango, COFAA, Instituto Politecnico Nacional,
Apartado Postal 738, Durango, Dgo., 34000, Mexico

ABSTRACT

Chaboissaea includes four species, three occurring in Mexico and one in Argentina and Bolivia. Allozyme data were used to evaluate the genetic diversity within and among populations of *Chaboissaea atacamensis*, *C. decumbens*, *C. ligulata*, and *C. subbiflora*. Electrophoretic examination of 23 putative enzyme loci in 22 populations revealed that the diploid species (*C. atacamensis*, *C. ligulata*, *C. subbiflora*) are highly variable genetically (P ranging from 0.56 to 0.71; H ranging from 0.44 to 0.46) and show high levels of genetic diversity (F ranging from -0.30 to -0.70). These values are frequently encountered in outcrossing plants, where genetic variation is seques-tered primarily within populations. The highest conspecific allozymic similarity occurred between *C. atacamensis* and *C. subbiflora* ($I = 0.81$). It seems likely that these two species are the most derived diploid members of the genus and that the migration of the progenitor of *C. atacamensis* to South America has occurred recently. The annual habit found in the three species, appears to have arisen as a single event.

RESUMEN

Chaboissaea comprende cuatro especies, de las cuales tres se encuentran en México y una en la Argentina y Bolivia. Mediante el análisis de alozimas se evaluó la di-versidad genética dentro y entre poblaciones de *Chaboissaea atacamensis*, *C. decum-bens*, *C. ligulata*, y *C. subbiflora*. El examen electroforético de 23 loci putativo en-zimáticos en 22 poblaciones reveló que las especies diploides (*C. atacamensis*, *C. ligulata*, y *C. subbiflora*) tienen una alta variabilidad genética (P varía de 0.56 a 0.71; H varía de 0.44 a 0.46; F varía de -0.30 a -0.70), indicativa de la existencia de polinización cruzada. Esta variación se encuentra principalmente dentro de las po-blaciones. Se encontró mayor similitud alozimica entre *C. atacamensis* y *C. subbiflora* ($I = 0.81$). Probablemente estas dos especies diploides sean derivadas de un ancestro común y la migración de *C. atacamensis* a Sudamérica ha sido reciente. El hábito anual, común a las tres especies, muestra que probablemente se originaron al mismo tiempo.

Chaboissaea Fourn. is a New World genus that includes four spe-cies, three ranging from northwestern Chihuahua to Distrito Federal, Mexico and one occurring in northwestern Argentina and western Bolivia. Based on morphological resemblance, allozymic similarities

(Peterson et al. 1993), and shared chloroplast DNA restriction site mutations (Duvall et al. 1994), the genus is firmly embedded in the subtribe Muhlenbergiinae, along with *Bealia* Scrib. in Hack., *Blepharoneuron* Nash, *Lycurus* Kunth, *Muhlenbergia* Schreb., and *Pereilema* Presl.

Chaboissaea differs from other genera of Eragrostideae (sensu Clayton and Renvoize 1986) by having gray to grayish-yellow spikelets with one or two (occasionally three) florets per spikelet, with the lower floret perfect and the upper floret staminate or sterile, and by its base chromosome number of $x = 8$ (Peterson and Annable 1992). In the Eragrostideae the base chromosome number is generally 10, and only *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Crypsis* Ait., *Dasyochloa* Willdenow ex Rydberg, *Erioneuron* Nash, and *Munroa* Torrey have a base number of 8 (Gould 1958; Peterson 1988, 1989; Peterson and Annable 1990; Peterson et al. 1993; Reeder 1967, 1968, 1971, 1977; Reeder and Reeder 1988; Tateoka 1961).

Chromosome counts reported for *Chaboissaea atacamensis* (Parodi) P. M. Peterson & Annable, *C. ligulata* Fourn., and *C. subbiflora* (Hitchc.) Reeder & C. Reeder indicate these species are diploid ($2n=16$), although *C. subbiflora* possesses an aneuploid series of $2n=14, 16, 18$ (Peterson and Annable 1992; Reeder 1967, 1968; Reeder and Reeder 1988). The fourth species, *C. decumbens* (Swallen) Reeder & C. Reeder, is a tetraploid ($2n=32$) based on chromosome counts secured from individuals of a single population in two successive years (Reeder and Reeder 1988).

Three species of *Chaboissaea* are annual with upright to decumbent culms. The fourth species, *C. ligulata*, is a tufted perennial. Previously known only from the Provinces Jujuy and Salta, Argentina (Peterson and Annable 1992), *C. atacamensis* has recently been collected in the Departments of La Paz (Peterson and Soreng 13211 at AAU, BH, CONC, K, LPB, US), Oruro (Peterson, Annable, Soreng, and Laegaard 12740 at AAU, BH, CONC, K, LPB, US), and Potosí, Bolivia. *Chaboissaea atacamensis* occurs from approximately 16° to 25° S latitude along the high-elevation (2900–4000 m) altiplano in seasonally wet marshes, meadows, moist clay flats, margins of ephemeral pools, gravelly roadside pools, and sandy margins of lagoons. The other three species of *Chaboissaea* are endemic to Mexico where they occur at 1900–2600 m along drainage ditches, irrigation canals, gravelly alkaline flats, and meadows in blackish clay soil often in muddy water. In Mexico, *Chaboissaea ligulata* is the most wide ranging, occurring from Chihuahua to Distrito Federal (19° to 27° N latitude) and is often sympatric with either *C. decumbens* or *C. subbiflora*. The distribution of *C. decumbens* is restricted to two locations in western Chihuahua. *Chaboissaea subbiflora* is found only within a 70 km radius of the city of Durango.

A phylogeny of the genus based on 13 morphological character

suggested that a common ancestor of the widespread perennial and most basal taxon, *C. ligulata*, was also ancestral to the annual endemics, which evolved/radiated subsequently. (Peterson and Annable 1992). *Chaboissaea decumbens* and *C. atacamensis* were hypothesized to be the most derived taxa of the genus, and shared a common ancestor with *C. subbiflora* in a cladogram with the following topology (*C. ligulata* (*C. subbiflora* (*C. atacamensis*, *C. decumbens*))). Given this phylogenetic hypothesis it was postulated that the genus arose in north-central Mexico from perennial ancestors and then migrated to South America via long distance dispersal, or by jumping from "islands" of similar habitat (Raven 1963; Thorne 1972; Peterson and Annable 1992). The paucity of morphological variation among the annual species also suggests that the migration event of *C. atacamensis* to South America could be of recent origin. An alternative hypothesis might be stabilizing selection, where the extant phenotype/genotype is adapted to a particular ecogeographical niche.

Intraspecific and congeneric amphitropical disjuncts can only be understood from a "hemispheric perspective." Among the Eragrostideae there are 16 genera with disjunct sister species distributed in North and South America (Allred 1981; Peterson et al. in prep.). Fifteen species in the Eragrostideae occur on both continents as intraspecific north/south temperate disjuncts.

Similar studies of allozyme variation in the Mexican endemics, *Bealia mexicana* Scrib. in Beal., *Muhlenbergia argentea* Vasey, and *M. lucida* Swallen, revealed that all three species have relatively high intraspecific genetic variability (H ranging from 0.19 to 0.26) and high levels of genetic diversity (F ranging from 0.073 to -1.000) indicative of mixed mating and/or outcrossing plants (Peterson et al. 1993). Mean genetic identity values for pairwise comparisons of these three taxa indicated that *Bealia* was more similar to *M. argentea* than were the two species of *Muhlenbergia*.

The present study, the first analysis of soluble enzymes in *Chaboissaea*, was initiated to estimate the genetic diversity within and among populations of *C. atacamensis*, *C. ligulata*, and *C. subbiflora*. We also hoped to gain new insights into the phytogeographical history and evolutionary processes operating in sister taxa with amphitropical disjunct distributions. An important goal was to ascertain whether interspecific genetic similarity as estimated by allozymic loci corresponds with systematic relationships based on morphology.

METHODS

Twenty-three populations of the four species of *Chaboissaea* were sampled from sites representing each species' known geographic range. Two hundred fifteen individuals from eight populations of

TABLE 1. FIELD COLLECTIONS OF *BEALIA MEXICANA*, *MUHLENBERGIA ARGENTEA*, *M. LUCIDA*, *CHABOISSAEA DECUMBENS*, *C. LIGULATA*, AND *C. SUBBIFLORA* ANALYZED BY ENZYME ELECTROPHORESIS. Voucher specimens are deposited at US.

B. mexicana. MEXICO. **Chihuahua**: Parque Natural Cumbres de Majalca, W of Cumbres de Majalca, Peterson, Annable & Herrera 7981.

C. atacamensis. ARGENTINA. **Jujuy**: W of Abra Pampa at Rio Miraflores Puentte, Peterson & Annable 10294; S of La Quiaca, Peterson & Annable 10300; W of La Quiaca, Peterson & Annable 10319; NW of Cieneguillas, Peterson & Annable 10323; S of Cieneguillas, Peterson & Annable 10327; NW of Abra Pampa, Peterson & Annable 10337; **Salta**: Nevado de Cachi, Ruinas Las Pailas, Peterson, Annable & Morrone 10183. BOLIVIA. **Potosí**: N of Villazón, Peterson & Annable 11869.

C. decumbens. MEXICO. **Chihuahua**: W of Cuauhtémoc, Peterson & Annable 7983, 9587.

C. ligulata. MEXICO. **Chihuahua**: N of Cuauhtémoc, Peterson & Annable 8111. **Durango**: N of Durango, Peterson 9635; E of Durango, Peterson 9650. **Guanajuato**: SE of Ojuelos de Jalisco, Peterson 9682; SE of San Filipe, Peterson 9685; NE of Leon, Peterson 9697. **Jalisco**: E of Aguascalientes, Peterson 9680. **Zacatecas**: E of Ojuelos de Jalisco, Peterson 9681.

C. subbiflora. MEXICO. **Durango**: N of Durango, Peterson & Annable 8266; Peterson 9619, 9630, 9637; NE of Durango, Peterson 9651; S of Durango, Peterson 9652.

Muhlenbergia lucida. MEXICO. **Chihuahua**: Parque Natural Barranca del Cobre, S of Creel, Peterson, Annable & Herrera 8029.

C. atacamensis, 51 individuals from a single population of *C. decumbens* sampled in two successive years, 210 individuals from eight populations of *C. ligulata*, and 163 individuals from six populations of *C. subbiflora* were examined for electrophoretic variation (Table 1). Fresh leaf blades or entire plants, if small, were collected in the field, placed in 3.6 or 5.0 ml (Nunc) cryotubes, and frozen on site in liquid nitrogen.

Sample preparation and electrophoresis of enzymes followed the general methodology of Morden et al. (1987). Approximately 300 mg of mature tissue from each plant was homogenized in up to 25 drops of grinding buffer (Morden et al. 1987) together with about 50 mg of sea sand to enhance disruption of cells. Extracts were absorbed into 2 × 11 mm Whatman filter paper wicks and stored at -80°C. Electrophoresis was conducted in the four gel/buffer systems of Morden et al. (1987): L, M, N, and T; however, starch content was modified to optimize gel handling characteristics and improve resolution. All gels consisted of Sigma starch with a total starch content of 10.6%, 12.0%, 11.5%, and 12.0% for the L, M, N, and T systems, respectively. For each population, samples from all individuals were included together on the same gel. Selected individuals from different populations were then analyzed together for purposes of interspecific and interpopulational comparisons. Gels were sliced and stained for the following 14 enzymes: aspartate aminotransferase

(AAT), aconitase (ACO), adenylate kinase (ADK), aminopeptidase (AMP), fructokinase (FRK), glutamate dehydrogenase (GDH), glutamate-pyruvate transaminase (GPT), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase (SAD), and triose phosphate isomerase (TPI). The genetic basis of interpreting the banding pattern was based on the known subunit structure and conserved number of isozymes at the diploid level. Only the faster migrating bands of IDH, assumed to be the plastid form which are encoded in the nucleus, were surveyed (Gottlieb 1982; Weeden and Wendel 1989). Loci were designated sequentially with the most anodally-migrating isozyme designated 1, the next 2, and so on. Alleles were designated sequentially with the most anodally-migrating allele given an *a*, the next *b*, and so on.

Values for Nei's (1972) genetic identity (*I*) and distance measures were computed for pairwise comparisons using BIOSYS-1 (Swofford and Selander 1989). Standard measures of genetic variation (Table 3) were computed for the diploids, *C. atacamensis*, *C. ligulata*, and *C. subbiflora*, including mean number of alleles per locus (*A*), proportion of polymorphic loci (*P*), mean heterozygosity (*H*), and mean fixation index (*F*) which measures the deviation of genotypic proportions from Hardy-Weinberg expectations (Wright 1965). The polyploid, *Chaboissaea decumbens* was omitted from these analyses because diversity statistics are theoretically appropriate only for plants that genetically have the characteristics of diploids. The distribution of genetic variation within the three diploid species was determined using F-statistics (Table 4) where F_{IS} is the fixation index within populations, F_{IT} is the overall fixation index or inbreeding coefficient, and F_{ST} measures the degree of differentiation among populations (Wright 1965, 1969; Jain and Workman 1967). The patristic distance matrix was calculated using the Prevosti distance index (Wright 1978) and after optimization of branch lengths, a corresponding Wagner tree or phylogeny (Fig. 1) was produced using *Bealia mexicana* and *Muhlenbergia lucida* as outgroups (Swofford and Selander 1989).

RESULTS

Fourteen enzymes encoded by 23 putative loci were consistently scorable by starch gel electrophoresis: AAT-2, AAT-3, ACO-1, ACO-2, ADK-1, ADK-2, AMP-2, FRK-1, FRK-3, GDH, GPT, IDH-1, MDH-1, MDH-2, MDH-3, PGD-1, PGD-2, PGI-1, PGI-2, PGM-1, SAD, TPI-1, TPI-2. Several putative loci, viz., AAT-1, AMP-1, FRK-2, and GPT-2, were not scored because of faint or inconsistent staining. Allele frequencies for all 24 populations surveyed in this

TABLE 2. INTRASPECIFIC ALLELE FREQUENCY DATA FOR 23 POLYMORPHIC LOCI AMONG THE FOUR SPECIES OF *CHABOISSAEA*.

Locus	Allele	<i>C. atacamensis</i>	<i>C. ligulata</i>	<i>C. subbiflora</i>
AAT-2	a	0.840	0.288	0.601
	b	0.160	0.548	0.266
	c	0.000	0.164	0.133
AAT-3	a	1.000	0.754	0.468
	b	0.000	0.246	0.178
	c	0.000	0.000	0.276
	d	0.000	0.000	0.078
ACO-1	a	0.010	0.139	0.014
	b	0.981	0.847	0.928
	c	0.009	0.014	0.058
ACO-2	a	0.005	0.019	0.029
	b	0.484	0.603	0.436
	c	0.509	0.378	0.510
	d	0.002	0.000	0.025
ADK-1	a	0.396	0.528	0.486
	b	0.542	0.472	0.514
	c	0.062	0.000	0.000
ADK-2	a	0.498	0.500	0.335
	b	0.467	0.500	0.380
	c	0.035	0.000	0.285
AMP-2	a	0.000	0.069	0.107
	b	0.002	0.393	0.332
	c	0.659	0.516	0.476
	d	0.339	0.022	0.085
FRK-1	a	0.995	0.975	0.938
	b	0.005	0.025	0.062
FRK-3	a	0.406	1.000	0.968
	b	0.594	0.000	0.032
GDH	a	0.000	0.383	0.007
	b	1.000	0.585	0.993
	c	0.000	0.032	0.000
GPT	a	0.995	0.628	0.929
	b	0.005	0.367	0.071
	c	0.000	0.005	0.000
IDH	a	0.000	0.529	0.215
	b	0.558	0.266	0.305
	c	0.442	0.072	0.469
	d	0.000	0.133	0.011
MDH-1	a	0.107	0.280	0.040
	b	0.396	0.232	0.460
	c	0.497	0.488	0.500
MDH-2	a	0.933	0.914	0.362
	b	0.067	0.086	0.555
	c	0.000	0.000	0.083
MDH-3	a	0.498	0.440	0.500
	b	0.502	0.454	0.500
	c	0.000	0.070	0.000
	d	0.000	0.036	0.000
PGD-1	a	1.000	1.000	0.976
	b	0.000	0.000	0.024

TABLE 2. Continued.

Locus	Allele	<i>C. atacamensis</i>	<i>C. ligulata</i>	<i>C. subbiflora</i>
PGD-2	a	0.012	0.014	0.362
	b	0.488	0.549	0.153
	c	0.500	0.437	0.485
PGI-1	a	0.500	0.202	0.204
	b	0.500	0.288	0.186
	c	0.000	0.283	0.610
	d	0.000	0.227	0.000
PGI-2	a	0.287	0.500	0.500
	b	0.213	0.500	0.500
	c	0.500	0.000	0.000
PGM	a	0.965	0.739	0.965
	b	0.028	0.245	0.035
	c	0.007	0.016	0.000
SAD	a	0.235	0.000	0.000
	b	0.228	0.000	0.052
	c	0.000	0.163	0.179
	d	0.002	0.254	0.435
	e	0.535	0.583	0.334
TPI-1	a	0.000	0.034	0.006
	b	1.000	0.947	0.816
	c	0.000	0.019	0.175
TPI-2	a	0.000	0.158	0.003
	b	0.002	0.325	0.164
	c	0.998	0.517	0.833

study appear in Appendix 1. Only segregating loci (polymorphic for 2 or more alleles) in the diploids were used to determine the genetic variation in populations and taxa, and for calculating F-statistics (Tables 3 and 4). The following non-segregating loci that were fixed for a pair of different alleles, indicative of fixed heterozygosity, were removed from the analysis: PGI-1 (*C. atacamensis*); ADK-2, PGI-2 (*C. ligulata*); and MDH-3, PGI-2 (*C. subbiflora*). All putative loci were used to generate the Wagner tree. Although not included in the genetic analysis, *C. decumbens* had eight non-segregating loci (ACO-2, ADK-1, ADK-2, IDH, MDH-2, MDH-3, PGD-2, PGI-2), indicating fixed heterozygosity.

Intraspecific allele frequencies at 23 variable loci are given in Table 2. The number of alleles per polymorphic locus ranged from two at FRK-1, FRK-3, and PGD-1 to five at SAD (Table 2). The greatest number of alleles per locus observed in a population was four (*C. ligulata*: population 9680-MDH-3; 9682-IDH; 9685-AMP, IDH; 9697-AMP and *C. subbiflora*: 8266-ACO-2; 9619-ACO-2; 9630-AMP, SAD; 9637-AMP, SAD; 9651-ACO-2, IDH; 9652-ACO-2, AMP). Four, three, and two unique alleles were detected in *C. ligulata*, *C. subbiflora*, and *C. atacamensis*, respectively (Table 2, 4).

TABLE 3. GENETIC VARIATION IN POPULATIONS AND TAXA OF *CHABOISSAEA ATACAMENSIS*, *C. LIGULATA*, AND *C. SUBBIFLORA*: sample size (n); mean number of alleles per locus (A); mean proportion of polymorphic loci (P); 95% criterion, mean heterozygosity (H), direct count estimate; and mean fixation index (F).

Taxon & coll. no.	n	A	P	H	F
<i>C. atacamensis</i>	10183	27	1.7	0.64	0.451
<i>C. atacamensis</i>	10294	26	2.0	0.68	0.393
<i>C. atacamensis</i>	10300	27	1.8	0.64	0.411
<i>C. atacamensis</i>	10319	26	1.6	0.55	0.458
<i>C. atacamensis</i>	10323	26	1.5	0.46	0.371
<i>C. atacamensis</i>	10327	26	1.6	0.50	0.490
<i>C. atacamensis</i>	10337	26	1.5	0.50	0.476
<i>C. atacamensis</i>	11869	31	1.7	0.56	0.490
<i>C. ligulata</i>	8111	26	1.5	0.38	0.321
<i>C. ligulata</i>	9635	26	2.1	0.86	0.434
<i>C. ligulata</i>	9650	27	2.4	0.91	0.462
<i>C. ligulata</i>	9680	26	2.1	0.67	0.496
<i>C. ligulata</i>	9681	26	1.9	0.62	0.520
<i>C. ligulata</i>	9682	28	2.2	0.76	0.503
<i>C. ligulata</i>	9685	25	2.4	0.81	0.470
<i>C. ligulata</i>	9697	26	2.2	0.71	0.443
<i>C. subbiflora</i>	8266	24	2.0	0.67	0.389
<i>C. subbiflora</i>	9619	27	2.2	0.76	0.527
<i>C. subbiflora</i>	9630	29	2.3	0.71	0.462
<i>C. subbiflora</i>	9637	27	2.4	0.71	0.526
<i>C. subbiflora</i>	9651	30	2.2	0.71	0.367
<i>C. subbiflora</i>	9652	26	2.2	0.71	0.430
Within taxa					
<i>C. atacamensis</i>	215	1.7	0.56	0.44	-0.70
<i>C. ligulata</i>	210	2.1	0.71	0.46	-0.41
<i>C. subbiflora</i>	163	2.2	0.71	0.45	-0.30

There were no unique alleles in *C. decumbens*, and none of the unique alleles in the other three taxa were fixed.

The mean number of alleles per locus (A) within populations ranged from 1.5 to 2.4 and the mean proportion of polymorphic loci (P) ranged from 0.38 to 0.91 (Table 3). The mean heterozygosity (H), direct count estimate, ranged from 0.321 to 0.520, indicating a high level of heterozygosity at most polymorphic loci. The mean fixation index (F) within populations, or inbreeding coefficient, ranged

TABLE 4. SUMMARY OF F-STATISTICS AND UNIQUE ALLELES WITHIN POPULATIONS OF *CHABOISSAEA ATACAMENSIS*, *C. LIGULATA*, AND *C. SUBBIFLORA*.

Taxon	F_{is}	F_{it}	F_{st}	Unique alleles
<i>C. atacamensis</i>	-0.785	-0.530	0.143	2
<i>C. ligulata</i>	-0.583	-0.095	0.288	4
<i>C. subbiflora</i>	-0.421	-0.143	0.195	3

TABLE 5. MEAN GENETIC IDENTITY VALUES (NEI 1972) AND RANGES FOR PAIRWISE COMPARISONS OF POPULATIONS OF *CHABOISSAEA ATACAMENSIS*, *C. LIGULATA*, AND *C. SUBBIFLORA*.

Taxa	<i>C. atacamensis</i>	<i>C. ligulata</i>	<i>C. subbiflora</i>
<i>C. atacamensis</i>	0.94 (0.89–0.99)	0.77 (0.67–0.89)	0.81 (0.70–0.88)
<i>C. ligulata</i>		0.82 (0.64–0.90)	0.78 (0.69–0.90)
<i>C. subbiflora</i>			0.88 (0.78–0.93)

from -0.169 to -0.907, indicating a significant deviation from Hardy-Weinberg expectations. Within taxa level means of P , H , and F were also high, and ranged from 0.56 to 0.71, 0.44 to 0.46, and -0.30 to -0.70, respectively.

Partitioning of genetic diversity, or the fixation of alleles at different hierachial levels, within and among populations of each diploid species was determined using F -statistics where the fixation index within populations (F_{IS}) ranged from -0.421 to -0.785 (Table 4). The amount of genetic diversity among populations within each species (F_{ST}) ranged from 0.143 to 0.288 and the overall fixation index (F_{IT}) ranged from -0.095, to -0.530. Summary F_{ST} values within each species are statistically significant at the 0.001 probability level (Pearson chi-square) indicating that each population within a species differs from other populations. For all three species, the primary component of F_{IT} was F_{IS} , i.e., the F_{ST} values were much smaller. This indicates greater heterogeneity within populations than among them.

Mean genetic identities among populations within each species were quite variable, ranging from 0.82 in *C. ligulata* to 0.94 in *C. atacamensis* (Table 5). Genetic identities between species ranged from 0.77 between *C. atacamensis* and *C. ligulata* to 0.81 between *C. atacamensis* and *C. subbiflora*. A tally of alleles held in common indicates that *C. decumbens* shares 37 alleles with *C. ligulata*, 36 with *C. atacamensis* and 36 with *C. subbiflora*.

A single Wagner tree (Fig. 1) summarizes the interpopulational relationship based on genetic distance values. Based on morphological similarities and allozymic resemblance (Peterson et al. 1993), *Muhlenbergia lucida* was chosen as an outgroup. Allozymic, morphological, and chloroplast restriction site data (Duvall et al. 1994) were also available for *Bealia mexicana*, another outgroup taxon. When using *Bealia mexicana* independently, or in combination with *Muhlenbergia lucida*, as outgroups a tree with a topology identical to that of Figure 1 was generated. When using *M. lucida* independently as an outgroup a tree with similar topology to Figure 1 was generated. However, *C. atacamensis* is portrayed as paraphyletic

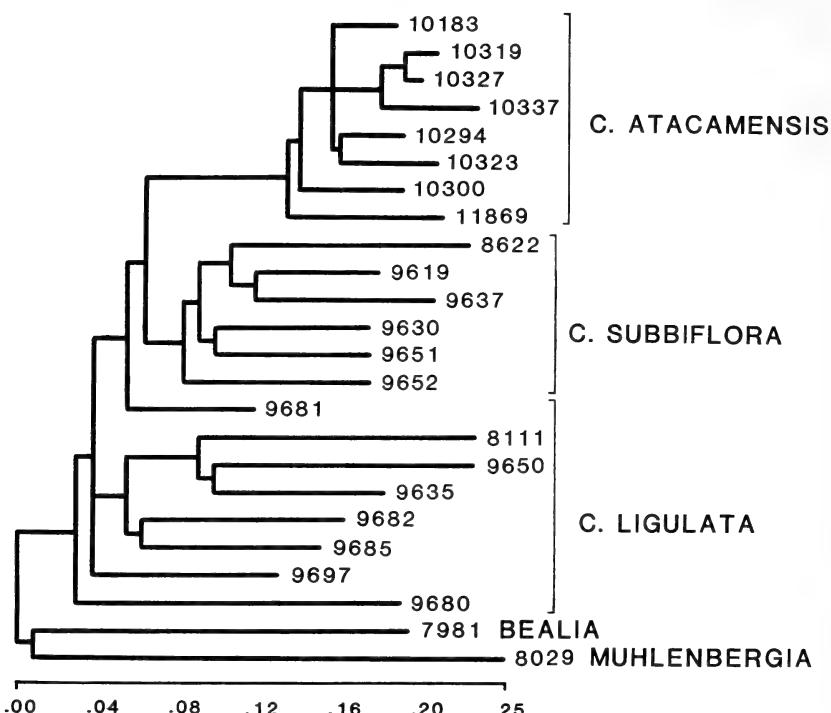


FIG. 1. Wagner tree showing genetic distance among populations of *Chaboissaea atacamensis*, *C. ligulata*, and *C. subbiflora*. *Bealia mexicana* and *M. lucida* was designated as the outgroup. Correlation coefficient = 0.95; length = 2.5; numbers refer to population collections given in Table 1; scale indicates distance from root.

instead of *C. ligulata* and a single population of *C. atacamensis* (11869) is aligned near the base of the tree near the root.

DISCUSSION

Population genetics. Populations of *C. atacamensis*, *C. ligulata*, and *C. subbiflora* contain high levels of genetic variation, comparable to that found in outcrossing plant species (Hamrick et al. 1979; Hamrick and Godt 1989). This is reflected in the high mean proportion of polymorphic loci (0.56–0.71) per species and high heterozygosity levels (0.44–0.46) per species (Table 3). The predominantly negative mean fixation indices per species (−0.30 to −0.70) indicate a consistent excess of heterozygotes.

The tetraploid, *C. decumbens*, displayed the fixed heterozygote pattern for eight enzyme systems which is typical of most allopolyploids. Although these data strongly suggest an allopolyploid origin

of *C. decumbens*, formal genetic analyses are necessary to determine mode of inheritance. There were no unique alleles in *C. decumbens*, suggesting that it may have evolved more recently than other members of the genus. *Chaboissaea ligulata* may represent one of the progenitors of *C. decumbens*, since both share the most alleles in common.

All three diploid species possess high levels of genetic heterogeneity (Tables 3, 4) within populations (negative F_{IS} values) and exhibit lower levels of genetic fixation among populations (F_{ST}). The highest level of genetic heterogeneity was found in the widespread, South American annual, *C. atacamensis* ($F = -0.70$, $F_{IS} = -0.785$), followed by the widespread perennial, *C. ligulata* ($F = -0.41$, $F_{IS} = -0.583$), and the local endemic, *C. subbiflora* ($F = -0.30$, $F_{IS} = -0.421$). Overall measures of deviation from Hardy-Weinberg expectations indicative of an excess of heterozygotes were found in *C. atacamensis* ($F_{IS} = -0.785$) and to a lesser extent in *C. ligulata* ($F_{IS} = -0.583$) and *C. subbiflora* ($F_{IS} = -0.421$). In *C. ligulata*, more of the observed genetic variation is apportioned among populations ($F_{ST} = 0.288$) than in either *C. atacamensis* ($F_{ST} = 0.143$) or *C. subbiflora* ($F_{ST} = 0.195$). This may be a consequence of the perennial habit of *C. ligulata* that potentially could allow for the maintenance of greater heterogeneity between populations over time and/or that allopatric speciation is occurring more rapidly in this species.

Species relationships. The interpopulation mean genetic identity values (Table 5) within each of the three species are quite variable. *Chaboissaea atacamensis* has high interpopulational identity values similar to those reported for other intraspecific plant populations of 0.94 (Gottlieb 1977; 1981; Crawford 1983, $I = 0.95$). Interpopulational identity values for *C. ligulata* ($I = 0.82$) and *C. subbiflora* ($I = 0.88$) are lower, although not nearly as low as the average reported for congeneric species (Gottlieb 1981; $I = 0.67$).

Morphologically, *C. atacamensis* and *C. decumbens* share three characteristics: small anthers (<1.2 mm long), anthers olivaceous or greenish, and blades with sinuous-walled costal short cells (Peterson and Annable 1992). These two species were previously hypothesized as the most derived members of the genus (Peterson and Annable 1992). Since *C. atacamensis* and *C. subbiflora* each share 36 alleles with *C. decumbens*, it seems likely that one progenitor of *C. decumbens* was a common ancestor of these two species.

It is interesting to note that the genetic similarity among populations of *C. ligulata* ($I = 0.82$) is about the same as the similarity between *C. atacamensis* and *C. subbiflora* ($I = 0.81$). This could be a result of the recent migration or speciation event involving these last two taxa because their soluble enzymes and their morphology are quite similar. It is also quite possible that populations of *C.*

ligulata are in the process of local genetic diversification in direct response to different ecological factors, i.e., ecotypic differentiation.

Although the Wagner tree is based on a distance matrix, the topology will be interpreted in a phylogenetic context for the following discussion. There is a general clade that represents each species (Fig. 1), except where *C. ligulata* (population 9681) shares a most recent common ancestor with the *C. subbiflora* clade and *C. ligulata* (populations 9680, 9697) is a sister group to all other populations of *Chaboissaea*. None of these three "misplaced" populations display any morphological or ecological differentiation that might account for their unusual alignment.

When using *Bealia* independently and/or in combination with *M. lucida* as outgroups, *C. atacamensis* and *C. subbiflora* are portrayed as the most derived members of the genus. *Chaboissaea ligulata* is most basal with respect to the other species in the genus. This finding is congruent with a cladistic analysis based on morphology (Peterson and Annable 1992). When *M. lucida* is independently used as the outgroup, *C. ligulata* and *C. subbiflora* are the most derived members of the genus and *C. atacamensis* is basal. Evidence from chloroplast DNA restriction site studies (Duvall et al. 1994) indicates that *Bealia* and *Muhlenbergia* are suitable outgroups and that *Muhlenbergia* may be the closest sister to *Chaboissaea*. However, *M. lucida* was not one of the species included in the DNA analysis and *Muhlenbergia* is depicted as being para- or polyphyletic.

These two distinct hypotheses of the phylogenetic relationship among the species in *Chaboissaea* lead to completely different evolutionary scenarios. One hypothesis suggests that the perennial habit and unawned paleas are plesiomorphic and that a common ancestor shared with *C. ligulata* gave rise to the annual species followed by subsequent radiation to South America of *C. atacamensis* or at least an intermediate ancestor to *C. atacamensis*. Because *C. atacamensis* and *C. subbiflora* share a high genetic identity value ($I = 0.81$) and the genetic variation among populations for both species is low, they could have evolved recently along with the tetraploid, *C. decumbens*. The alternative hypothesis where *C. atacamensis* is the basal taxon, suggests that the annual habit and awned paleas are plesiomorphic. In the latter case we would still hypothesize that the genus arose in central Mexico because the greatest species diversity resides there today.

Since the genetic identity value between *C. atacamensis* and *C. subbiflora* is the highest among conspecific comparisons ($I = 0.81$), the allozyme evidence presented here suggests that these species are of recent origin when compared to others in the genus. Therefore, the more parsimonious explanation favors a phylogeny where *C. atacamensis* and *C. subbiflora* are the most derived members of the genus, and that subsequent reticulate evolution of *C. decumbens* has

occurred. A chloroplast DNA restriction site analysis is in progress which will perhaps provide additional insights into the hypothesized phylogeny of species within *Chaboissaea* (Sykes, Christensen, and Peterson, in prep.).

ACKNOWLEDGMENTS

This study was supported by grants from the Smithsonian Institution Research Opportunities and Scholarly Studies Funds, and the National Geographic Society. Special thanks are given to Carol R. Annable, Robert M. King, and Osvaldo Morrone for help collecting the specimens in the field; Melvin R. Duvall, Marjorie B. Knowles, and CRA for laboratory assistance; Zulma Rugolo de Agrasar for preparing the Spanish abstract; and J. Travis Columbus and Robert J. Soreng for reviewing the manuscript.

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APPENDIX 1. ALLELE FREQUENCIES FOR 24 POPULATIONS OF *CHABORSSAEA ATACAMENSIS* (A), *C. LIGULATA* (L), *C. SUBBIFLORA* (S), *BEALIA MEXICANA* (B), AND *MUHLENBERGIA LUCIDA* (M). Numbers following the lettercode refer to collection (see Tables 1, 3).

Locus/ allele	Populations						
	A10183	A10294	A10300	A10319	A10323	A10327	A10337
AAT-2							
a	1.000	1.000	.222	1.000	1.000	.500	1.000
b	.000	.000	.778	.000	.000	.500	.500
c	.000	.000	.000	.000	.000	.000	.000
AAT-3							
a	1.000	1.000	1.000	1.000	1.000	1.000	.981
b	.000	.000	.000	.000	.000	.000	.019
c	.000	.000	.000	.000	.000	.000	.000
d	.000	.000	.000	.000	.000	.000	.000
ACO-1							
a	.000	.077	.000	.000	.000	.000	.077
b	.963	.885	1.000	1.000	1.000	1.000	.923
c	.037	.038	.000	.000	.000	.000	.000
ACO-2							
a	.000	.038	.000	.000	.000	.000	.000
b	.500	.481	.389	.500	.500	.500	.962
c	.500	.462	.611	.500	.500	.500	.038
d	.000	.019	.000	.000	.000	.000	.000
ADK-1							
a	.500	.500	.167	.500	.500	.500	.500
b	.500	.500	.833	.500	.500	.500	.500
c	.000	.000	.000	.000	.000	.000	.000
ADK-2							
a	.500	.481	.500	.500	.500	.500	.500
b	.500	.385	.500	.500	.500	.355	.500
c	.000	.135	.000	.000	.000	.145	.000

APPENDIX 1. Extended.

Locus/ allele	Populations							M8029
	L9681	L9682	L9685	L9697	S8266	S9619	S9630	
AAT-2								
a	.019	.500	.060	.173	.583	.500	1.000	.500
b	.500	.500	.940	.615	.417	.500	.204	.442
c	.481	.000	.000	.212	.000	.000	.296	.000
AAT-3								
a	.500	1.000	1.000	1.000	.000	.444	1.000	.222
b	.500	.000	.000	.000	.125	.241	.000	.050
c	.000	.000	.000	.000	.500	.315	.000	.593
d	.000	.000	.000	.000	.375	.000	.000	.250
ACO-1								
a	.058	.000	.060	.019	.000	.000	.017	.017
b	.942	1.000	.940	.923	1.000	.981	.983	.704
c	.000	.000	.000	.058	.000	.019	.000	.296
ACO-2								
a	.077	.018	.060	.000	.021	.019	.000	.093
b	.442	.500	.440	.500	.458	.389	.345	.444
c	.481	.482	.500	.500	.500	.574	.655	.407
d	.000	.000	.000	.000	.021	.019	.000	.056
ADK-1								
a	.500	.500	.500	.500	.500	.500	.500	.417
b	.500	.500	.500	.500	.500	.500	.500	.583
c	.000	.000	.000	.000	.000	.000	.000	.000
ADK-2								
a	.500	.500	.500	.500	.792	.241	.069	.167
b	.500	.500	.500	.500	.208	.500	.431	.463
c	.000	.000	.000	.000	.000	.259	.500	.370

APPENDIX 1. Continued.

APPENDIX 1. Extended, Continued.

Locus/ allele	Populations							S9652	B7981	M8029
	L9681	L9682	L9685	L9697	S8266	S9619	S9630			
AMP-2										
	a	.000	.071	.240	.038	.000	.071	.148	.000	.423
	b	.385	.500	.160	.750	.542	.593	.196	.250	.058
	c	.615	.429	.540	.096	.458	.333	.464	.389	.733
FRK-1	d	.000	.000	.060	.115	.000	.074	.268	.111	.017
	a	1.000	.893	1.000	.981	1.000	1.000	.630	1.000	.983
	b	.000	.107	.000	.019	.000	.000	.370	.000	.827
	c	.000	.000	.000	.000	.000	.000	.000	.000	.740
FRK-3	a	1.000	1.000	1.000	1.000	1.000	1.000	.000	.017	.000
	b	.000	.000	.000	.000	.000	.000	.000	.000	.000
	c	.000	.000	.000	.000	.000	.000	.000	.000	.000
	d	.000	.000	.000	.000	.000	.000	.000	.000	.000
GDH	a	.000	.107	.020	.923	.042	.000	.000	.000	.000
	b	1.000	.893	.980	.077	.958	1.000	1.000	1.000	1.000
	c	.000	.000	.000	.000	.000	.000	.000	.000	.000
	d	.000	.000	.000	.000	.000	.000	.000	.000	.000
GPT	a	1.000	.071	.327	1.000	1.000	.926	.793	1.000	.967
	b	.000	.929	.635	.000	.000	.074	.207	.000	.033
	c	.000	.000	.038	.000	.000	.000	.000	.000	.115
	d	.000	.000	.000	.000	.000	.000	.000	.000	.000
IDH	a	.115	.429	.240	.500	.354	.389	.017	.241	.100
	b	.385	.196	.220	.269	.125	.130	.586	.278	.383
	c	.000	.268	.080	.231	.521	.481	.397	.481	.327
	d	.500	.107	.460	.000	.000	.000	.067	.000	.000

APPENDIX 1. Continued.

APPENDIX 1. Extended, Continued.

Locus/ allele	Populations							M8029
	L9681	L9682	L9685	L9697	S8266	S9619	S9630	
MDH-1	.115	.250	.160	.135	.000	.037	.052	.037
	.385	.250	.340	.365	.500	.463	.448	.500
	.500	.500	.500	.500	.500	.500	.500	.500
MDH-2	.885	.875	.980	.981	1.000	.500	.172	.500
	.115	.125	.020	.019	.000	.500	.328	.500
	.000	.000	.000	.000	.000	.000	.500	.000
MDH-3	.500	.500	.500	.481	.500	.500	.500	.500
	.500	.482	.320	.500	.500	.500	.500	.500
	.000	.000	.000	.000	.000	.000	.000	.000
PGD-1	.000	.018	.180	.019	.000	.000	.000	.000
	1.000	1.000	1.000	1.000	.854	1.000	1.000	1.000
	.000	.000	.000	.000	.146	.000	.000	.000
PGD-2	.000	.000	.000	.060	.000	.375	.278	.310
	.500	.500	.400	.500	.125	.222	.224	.111
	.500	.500	.540	.500	.500	.466	.500	.500
PGI-1	.135	.018	.020	.173	.042	.278	.172	.204
	.500	.196	.000	.000	.125	.037	.310	.093
	.365	.286	.480	.327	.833	.685	.517	.704
	.000	.500	.500	.500	.000	.000	.000	.000

APPENDIX 1. Continued.

Locus/ allele	Populations											
	A10183	A10294	A10300	A10319	A10323	A10327	A10337	A11869	L8111	L9635	L9650	L9680
PGI-2	a	.500	.389	.212	.500	.192	.500	.000	.500	.500	.500	.500
	b	.500	.111	.288	.000	.308	.000	.500	.500	.500	.500	.500
	c	.500	.500	.500	.500	.500	.500	.000	.000	.000	.000	.000
PPGM	a	.963	.846	.926	.981	1.000	1.000	1.000	1.000	.923	.722	.231
	b	.000	.154	.074	.000	.000	.000	.000	.000	.077	.204	.769
	c	.037	.000	.000	.019	.000	.000	.000	.000	.074	.000	.000
SAD	a	.037	.077	.093	.500	.019	.462	.385	.306	.000	.000	.000
	b	.037	.000	.093	.500	.019	.462	.404	.306	.000	.000	.000
	c	.000	.000	.000	.000	.000	.000	.000	.000	.385	.130	.250
TPP-1	d	.000	.019	.000	.000	.000	.000	.000	.000	.096	.037	.385
	e	.926	.904	.815	.000	.962	.077	.212	.387	.519	.833	.365
	a	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.192
TPP-2	b	1.000	1.000	1.000	.000	1.000	1.000	1.000	1.000	.981	.692	.115
	c	.000	.000	.000	.000	.000	.000	.000	.000	.019	.000	.037
	c	1.000	.981	1.000	1.000	1.000	1.000	1.000	1.000	.000	.000	.635

APPENDIX 1. Extended, Continued.

Locus/ allele	Populations							M8029
	L9681	L9682	L9685	L9697	S8266	S9619	S9630	
PGI-2								
a	.500	.500	.500	.500	.500	.500	.500	.000
b	.500	.500	.500	.500	.500	.500	.500	.500
c	.000	.000	.000	.000	.000	.000	.000	.500
PGM								
a	1.000	.054	.980	1.000	1.000	.931	.944	.933
b	.000	.893	.020	.000	.000	.069	.056	.067
c	.000	.054	.000	.000	.000	.000	.000	.000
SAD								
a	.000	.000	.000	.000	.000	.000	.000	.000
b	.000	.000	.000	.000	.000	.017	.204	.000
c	.096	.268	.060	.115	.021	.037	.397	.315
d	.404	.429	.300	.385	.479	.870	.345	.407
e	.500	.304	.640	.500	.500	.093	.241	.074
TPI-1								
a	.000	.000	.040	.038	.000	.000	.034	.000
b	1.000	1.000	.960	.942	.021	.981	.914	1.000
c	.000	.000	.000	.019	.979	.019	.052	.000
TPI-2								
a	.000	.000	.280	.000	.000	.017	.000	.000
b	.000	.054	.260	.000	.000	.483	.000	.000
c	1.000	.946	.460	1.000	1.000	.500	.500	1.000

**EUPHORBIA GENTRYI, A NEW SPECIES OF EUPHORBIA
SUBGENUS AGALOMA FROM NORTHWESTERN MEXICO**

VICTOR W. STEINMANN

Herbarium, 113 Shantz Building, University of Arizona,
Tucson, AZ 85721

THOMAS F. DANIEL

Department of Botany, California Academy of Sciences,
Golden Gate Park, San Francisco, CA 94118

ABSTRACT

Euphorbia gentryi, a new species from northwestern Mexico, is described and illustrated. The species is treated in subgenus *Agaloma* and is distinguished from its relatives in northwestern Mexico by the combination of its glabrous herbage; large, white appendages; and membranaceous, mostly linear leaves with short petioles. *Euphorbia hindsiana* is recognized as distinct from *E. californica*, and a key to *E. gentryi*, *E. misera*, *E. californica*, and *E. hindsiana* is presented.

RESUMEN

Se describe e ilustra *Euphorbia gentryi* como especie nueva del noroeste de México. Pertenece al subgénero *Agaloma* y se distingue por la combinación de su herbaje glabro; apéndices blancos y grandes; y hojas membranáceas con pecíolos cortos y con láminas generalmente lineares. Se reconoce *E. hindsiana* como especie distinta de *E. californica* y se presenta una clave para *E. gentryi*, *E. misera*, *E. californica*, y *E. hindsiana*.

In 1940, Howard Scott Gentry collected an unusual *Euphorbia* from basaltic slopes in northern Sinaloa, Mexico. Similar plants have since been collected in other localities in northwestern Mexico. Our studies over several years have convinced us that they represent a previously undescribed species. This species is described below, and its relationships to three other species are discussed.

***Euphorbia gentryi* V. W. Steinmann & T. F. Daniel, sp. nov. (Fig.**

1).—TYPE: MEXICO, Sonora, Mesa Masiaca, 6.5 km WNW of San José de Masiaca, ca. 26°46'N, 109°17'W, Sinaloan Thorn-scrub on steep basaltic slopes, ca. 200 m, 22 Nov 1993, V. W. Steinmann et al. 93-357 (holotype, CAS!; isotypes, ARIZ!, MEXU!, TEX!).

Differt a *E. californica* Benth. foliis angustioribus apice acutis vel acuminatis, petiolis quam laminis plerumque brevioribus, appendicibus albis 1.5–4.5 mm longis.

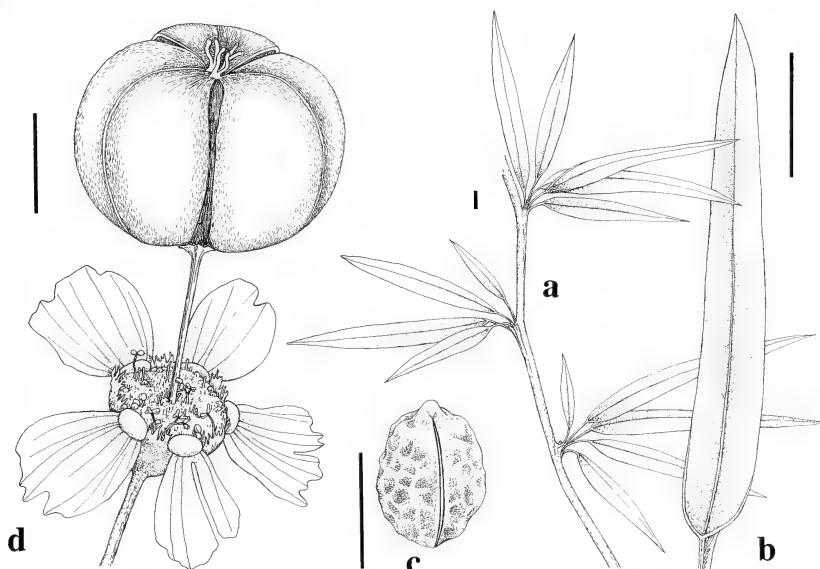


FIG. 1. *Euphorbia gentryi*. a, portion of vegetative branch (Daniel et al. 2538). b, leaf (Daniel et al. 2538). c, seed (Wiggins 13144). d, cyathium with capsule (Steinmann et al. 93-357). Scale bars = 2.5 mm.

Basally much-branched shrub to 4 m tall and to 10 cm in diameter at base; bark gray on older stems, dark and somewhat reddish on younger stems; twigs irregularly striate-ridged, glabrous, the young growth often covered with a thin waxy layer. Leaves (sometimes nearly or completely absent) alternate and often clustered on short lateral shoots, petiolate, stipulate; petioles 2–25 mm long, mostly shorter than blades, 0.2–0.4 mm in diameter, glabrous; stipules glandlike, dark, triangular, 0.2–0.6 mm long; blades linear to narrowly elliptic (to obovate), 15–42 mm long, (1.5) 3–12 (–18) mm wide, mostly 4–12 times longer than wide, glabrous, acute to tapered at base and apex, symmetric at base, margin at base of blade continuous across adaxial side of petiole. Cyathia borne in axillary (or terminal) pedunculate dichasria (sometimes clustered near shoot apex); bracts subfoliaceous (smaller than leaves), caducous; cyathia 1–12 (or more) per dichasium, pedunculate (peduncles 3–7 mm long), open-campanulate, 5–9 mm in diameter (including appendages), 1.7–3.5 mm in diameter (excluding appendages); lobes of involucres 0.5–1 mm long, apically erose to pectinate; glands 5, yellowish, transversely elongate-elliptic, 0.8–1.5 mm long (long axis); appendages of glands 5, conspicuous, white, ovate to circular to obovate, (1.1–) 1.5–4.5 mm long, 1.4–2.7 mm wide, entire, emarginate, shallowly lobed, or apically erose. Bracteoles among staminate flowers nu-

merous, densely pubescent. Staminate flowers ca. 25–40. Pistillate flowers subsessile to pedicellate, pedicels to 3.5 mm long, mostly erect in fruit; ovaries glabrous; styles divided from $\frac{1}{2}$ their length to nearly to base, yellowish, 0.8–1.2 mm long. Capsules green or somewhat reddish, 3-lobed, depressed globose, 3–5 mm long, 3.5–6 mm in diameter, glabrous. Seeds ecarunculate, whitish gray to brown, ovoid to subglobose, 2.2–3.5 mm long, 1.8–2.7 mm in diameter, foveolate.

PARATYPES: MEXICO, Sinaloa, hill near Hwy. 15 ca. 40 km N of Los Mochis and 1.6 km S of Los Natochis, *Daniel et al.* 2538 (ASU, DAV); Cerro Tecomate, W of Pericos, *Gentry* 5734 (ARIZ, DS, GH, NY, RSA); Bahía Topolobampo in Sierra Navachiste, *Gentry* 11430 (ARIZ); Cerro de Navachiste about Bahía Topolobampo, *Gentry* 14371 (ARIZ); Cerros del Fuerte, 18–24 mi N of Los Mochis, *Gentry* 14297 (ARIZ, US); ca. 2 km NW of Topolobampo, 25°58'N, 109°02'W, *Moran* 7580 (DAV, SD); ca. 2 km NW of Topolobampo, 25°58'N, 109°05'W, *Moran* 7586 (ARIZ, DAV, SD); hills 12.8 km S of Pericos, *Wiggins* 13144 (DS, SD). Sonora, ca. 10 mi S of Cd. Obregón, *Gentry* 14281 (ARIZ); near Hermosillo (Alamos), 29°05'N, 110°57'W, *Rauh* 25080 (SD); near summit of Cerro Cabaña, 5 mi E of Hwy. 15 at point 8 mi S of Cd. Obregón, 27°28'N, 109°46'W, *Sanders et al.* 1910 (UCR, DAV); summit of Cerro Prieto, vicinity of microwave station, 15 km E of Navojoa, ca. 27°15'N, 109°17'W, *Sanders et al.* 9276 (UCR); Mpio. Navojoa, summit of Cerro Masiaca, vicinity of microwave station, 2.5 km NE of Hwy. 15, 26°46.4'N, 109°17.9'W, *Sanders et al.* 12768 (ARIZ, UCR); 1.2 mi E of Mex. 15 at 11 mi S of Bacabachi, ca. 20 mi N of Sinaloa, *Soule and Krizman s.n.* (ARIZ); Cerro Prieto, ca. 14 km E of Navojoa, 27°05'N, 109°17'W, *Steinmann et al.* 93-113 (ARIZ, ASU, F, GH, MEXU, MO, NY); Cerro Prieto, ca. 9 mi E of Navojoa on Alamos Road, 27°05'N, 109°17'W, *Van Devender et al.* 92-167 (ARIZ).

Phenology. Flowering and fruiting: August–March; probably reproductive any time of the year that sufficient moisture is available. Likely drought deciduous.

Distribution and habitat. Northwestern Mexico (Sinaloa and Sonora); plants occur on, and are apparently restricted to, basaltic slopes of hills in thornscrub at elevations from 90 to 485 meters. On Cerro Prieto and Mesa Masiaca in southern Sonora, the plants are usually encountered in boulder fields.

Local name. “Vara leche” (*Gentry* 5734). This same name also appears on *Gentry* 5712, a specimen of *E. californica*.

The epithet of this species honors the late Howard Scott Gentry (1903–1993), who apparently was the first to collect it. Gentry’s

extensive collections from Sonora and Sinaloa have been the source of numerous undescribed species.

Euphorbia gentryi belongs to *Euphorbia* subgenus *Agaloma* (Raf.) House where its affinities lie with *E. californica* Benth., *E. misera* Benth., and *E. hindsiana* Benth. All four of these species share a shrubby habit with divaricate branching, young growth that is often covered with a thin waxy coating, short lateral shoots bearing alternate leaves, and foveolate seeds. They all occur in desertscrub and thornscrub of northwestern Mexico. *Euphorbia misera* also enters into southern California.

Among this group, *Euphorbia hindsiana*, known only from the Cape Region in Baja California Sur, frequently has been treated as *E. californica* var. *hindsiana* (Benth.) Wiggins (e.g., Wiggins 1955, 1964, 1980; Huft 1985). *Euphorbia californica* *sensu stricto* (i.e., var. *californica*) is known from Sonora, Sinaloa, Zacatecas, Baja California Sur, and the Islas Revillagigedo. The coriaceous (vs. membranaceous), yellow-green (vs. green) leaves with stout petioles usually shorter (vs. slender and usually longer) than the blades, and larger, white (vs. green to yellowish green) appendages of *E. hindsiana* seem sufficient characteristics to warrant its recognition as a species. It is not geographically separated from *E. californica* nor do there appear to be morphological intermediates between the two taxa.

The following key distinguishes *Euphorbia gentryi* from its relatives in northwestern Mexico:

1. Herbage, cyathia, ovaries, and capsules pubescent; base of leaf blade not continuous over adaxial side of petiole *E. misera*.
- 1' Herbage, cyathia, ovaries, and capsules glabrous; base of leaf blade usually continuous over adaxial side of petiole.
 2. Petioles often equaling or longer than blades; glandular appendages green to yellowish green, ≤ 1 mm long *E. californica*.
 - 2' Petioles usually shorter than blades; glandular appendages usually white, > 1 mm long.
 3. Leaf blades thick, coriaceous, pale yellowish green, subcircular to obovate to obcordate, rounded to truncate to emarginate at apex; Baja California Sur *E. hindsiana*.
 - 3' Leaf blades thin, membranaceous, dark green, linear to narrowly elliptic (to obovate), acute to tapered at apex; Sonora and Sinaloa .. *E. gentryi*.

Several specimens (i.e., *Gentry 11430*, *Gentry 14371*, and *Moran 7580*) from the vicinity of Bahía Topolobampo in northern Sinaloa, are vegetatively somewhat intermediate between typical *E. gentryi* and typical *E. californica*. The leaves are broad and the petioles vary from shorter to longer than the elliptic to obovate blades. However, the large glandular appendages are typical of *E. gentryi* to which these unusual specimens are tentatively referred. It remains to be determined whether these specimens represent a hybrid population,

an unusual geographic form of *E. gentryi*, or merely variation within that species. Other collections from near Topolobampo represent typical *E. gentryi* (i.e., Moran 7586) and typical *E. californica* (i.e., Hastings and Turner 64-105, DS). Another unusual collection (Sin-aloa: 7.5 mi SE of Guamuchil, Webster 19821, DAV) has very small (4–12 mm long and 2–7 mm wide), elliptic to obovate leaves with the petioles shorter than the blades. Its disposition remains uncertain and it is not included in the description above.

ACKNOWLEDGMENTS

We are grateful for the suggestions and/or support of G. Webster, R. McVaugh, A. Sanders, P. Martin, T. Van Devender, and R. Van Devender. We thank the curators of the following herbaria for providing loans or access to their collections: ARIZ, ASU, CAS, DAV, DS, NY, RSA, SD, and US. Daniel's field work in Mexico was supported, in part, by the Department of Botany and Microbiology of Arizona State University. The illustration was prepared by Jenny Speckels with support from the California Academy of Sciences.

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NEW COMBINATIONS FOR *EUPHORBIA* AND *DITAXIS* (*EUPHORBIACEAE*) IN NORTHWESTERN MEXICO AND SOUTHWESTERN UNITED STATES

VICTOR W. STEINMANN AND RICHARD S. FELGER
Herbarium, University of Arizona,
Tucson, AZ 85721

ABSTRACT

Euphorbia villifera var. *crepuscula* is elevated to specific status and *Ditaxis californica* is reduced to a variety of *D. serrata*.

RESUMEN

Euphorbia villifera var. *crepuscula* se eleva a estado específica y *Ditaxis californica* se reduce a una variedad de *D. serrata*.

During the course of our preparation of a synopsis of the Euphorbiaceae of Sonora, Mexico, and work on several local floras, the need for the following new taxonomic changes became apparent. We have seen all specimens cited here.

Euphorbia crepuscula* (L. C. Wheeler) comb. nov.—Euphorbia vilifera* Scheele var. *crepuscula* L. C. Wheeler, Contributions from the Gray Herbarium 127:61. 1939.

This species is quite distinct from *E. villifera* Scheele. The two share the character of having laterally compressed cocci, the distal part of which is empty, but as noted by Wheeler, there are a number of significant differences between them. *Euphorbia crepuscula* has linear or oblong-linear leaves, an epappilate epidermis, and seeds with distinct transverse ridges, while *E. villifera* has ovate to triangular-ovate leaves, a papillate epidermis, and seeds that are smooth to slightly wrinkled. Also, in *E. crepuscula* the bracteoles have fewer filiform, hairlike divisions than in *E. villifera*.

When Wheeler described this taxon as a variety of *E. villifera*, he seems to have placed too much emphasis on the carpel character. The affinities of *E. crepuscula* are not obvious, but the seeds, which possess transverse ridges and frequently whitened angles, bear striking similarity to *E. hyssopifolia* L. We know of only three collections of this species. The Sonora collections are in the southeastern part of the state.

Specimens examined. MEXICO: SONORA: Guirocoba, District

of Alamos, 13 Nov 1933, *Gentry 789M* (holotype, GH) [Guirocoba is at the boundary of tropical deciduous forest and oak woodland]. Mesa la Lagunita, 27°58'20"N, 109°06'30"W, 1100 m, Chihuahua oak woodland, basalt soil, 6 Nov 1986, *Martin et al. s.n.* (ARIZ). SINALOA: Cofradía, 22 Oct 1904, *Brandegee s.n.* (GH).

Ditaxis serrata (Torrey) A. A. Heller var. *californica* (Brandegee) comb. nov.—*D. californica* (Brandegee) Pax & K. Hoffm., Pflanzenreich 4, 147, 6:70. 1912.—*Argythamnia californica* Brandegee, Zoe 5:230. 1906.

This unusual *Ditaxis* is endemic to Shreve's (1951) Lower Colorado Desert subdivision of the Sonoran Desert. It occurs in southeastern California (Webster 1993), the east flanks of the Sierra Juárez in northeastern Baja California (Wiggins 1980), and northwestern Sonora (Felger 1992). The single collection from Sonora, consisting of two small plants, is disjunct about 200 km. It has not been found again in Sonora despite repeated searches at the same station and surrounding territory.

Ditaxis californica is here reduced to a variety of *D. serrata* because we find no difference between them other than the glabrous, naked condition of the former. *Ditaxis serrata* var. *californica* primarily occurs in the western part of the overall geographic range of *D. serrata*.

Wiggins (1964:785) pointed out the "pistillate calyx with a conspicuous glandlike callus just below each intersepalary sinus" as a key character for *D. californica*. This feature is present among the type collection and on many other specimens of var. *californica*, and is also variously present or absent on var. *serrata* as well as the very closely related *D. neomexicana* (Muell. Arg.) A. A. Heller. Among these three taxa there appear to be minor differences in the shape of the floral glands. However, these characters may well vary with seasonal or local environmental conditions. Another character of questionable significance is the shape of the stigma branches. This does not seem to be a diagnostic character as the stigma branches are usually terete in all three taxa or sometimes slightly flattened apically.

An annotation by Ivan M. Johnston on a specimen of var. *californica* collected in California (South base of Eagle Mts., Munz & Keck 4833 in 1922, POM) reads "This looks suspiciously like a glabrate form of *D. serrata*." Another California collection from the Colorado Desert (*Wolf 3048* in 1932, RSA) has three plants on the herbarium sheet. Two are glabrous (var. *californica*) and one is pubescent (var. *serrata*); these plants are strikingly similar apart from the presence or absence of hairs. An analogous situation occurs in Texas, with *D. humilis* Engelm. & A. Gray var. *laevis* Torrey being

a glabrous segregate of the hairy and more common and widespread var. *humilis*.

Specimens examined. USA: CALIFORNIA: Riverside Co., Marshall Canyon, 7 mi W of Coachella, 100 ft, April 1905, Hall 5796 (holotype of *Argythamnia californica*, UC; isotypes, UC and POM). MEXICO: SONORA: Puerto Peñasco, Casa García (ca. 3 km E of center of town), coastal dunes with annuals, 50 ft, 28 Mar 1980, Yatskievych 80-43 (ARIZ).

ACKNOWLEDGMENT

The authors thank the curators and staffs of the following herbaria for their assistance: ARIZ, GH, RSA-POM, UC.

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NICKEL ACCUMULATION BY SERPENTINE SPECIES OF *STREPTANTHUS* (BRASSICACEAE): FIELD AND GREENHOUSE STUDIES

A. R. KRUCKEBERG

Department of Botany, University of Washington,
Seattle, WA 98195

R. D. REEVES

Department of Chemistry and Biochemistry, Massey University,
Palmerston North, New Zealand

ABSTRACT

Hyperaccumulation of nickel by higher plants ($>1000 \mu\text{g/g}$ in tissue) is closely associated world-wide with serpentine soils. In North America, nine hyperaccumulators have been identified, some from analysis of herbarium samples. *Streptanthus polygaloides*, found earlier to be a hyperaccumulator on Sierra Nevada serpentines, merited further study. We report on field-collected samples and greenhouse cultures of this and other *Streptanthus* species. Fresh samples from eight serpentine sites all had more than $1000 \mu\text{g/g}$ of nickel (2430–18600 $\mu\text{g/g}$), clearly confirming the earlier results. Other serpentine *Streptanthus* spp., collected in the field or grown on serpentines in the greenhouse, had modest nickel levels and could be termed excluders. Greenhouse cultures of *S. polygaloides* on non-native serpentine soils also accumulated nickel in excess of $1000 \mu\text{g/g}$. Although field samples of *S. barbiger*, a Coast Range serpentine endemic, took up low amounts of nickel, this species grown on non-native serpentine soils accumulated nickel (69–1200 $\mu\text{g/g}$). This unusual result is discussed as are the ecological and evolutionary implications of nickel accumulation and nickel exclusion in *Streptanthus*.

Exceptional uptake of nickel by a small proportion of the plant species found on serpentine soils (derived from serpentinites and related ultramafic rocks) is now known to occur in many parts of the world. Nearly 200 species are known, in at least some of their occurrences, to contain more than $1000 \mu\text{g/g}$ Ni (dry weight basis), a level that has been set as the threshold for applying the term ‘hyperaccumulation’ (Brooks et al. 1977). The most recent comprehensive list of plant species exhibiting this behavior is that of Reeves (1992).

Serpentines occur in North America, both on the eastern seaboard from Georgia to Quebec and Newfoundland, and on the Pacific coast (California, Oregon, Washington, and British Columbia). Despite this rich display, and the occurrence of over a thousand plant species on North American serpentine soils, only nine taxa have been reported to exhibit nickel hyperaccumulation: *Streptanthus polygaloides* Gray (Reeves et al. 1981), three varieties of *Thlaspi montanum*

TABLE 1. RECORDS OF NICKEL HYPERACCUMULATION IN NORTH AMERICAN PLANTS.

Species	Locality	Nickel conc. ($\mu\text{g/g}$ dry wt.)	Reference
Asteraceae			
<i>Senecio pauperulus</i>	W. Newfoundland	1903	Roberts (1992)
<i>Solidago hispida</i>	W. Newfoundland	1023	Roberts (1992)
Brassicaceae			
<i>Streptanthus polygaloides</i>	California	1100–16,400	Reeves et al. (1981)
<i>Thlaspi montanum</i> var. <i>californicum</i>	Humboldt Co., Calif.	3850–11,600	Reeves et al. (1983)
var. <i>montanum</i>	California, Oregon, Washington	784–11,300	Reeves et al. (1983)
<i>var. siskiyouense</i>	Josephine Co., Oregon	3920–27,800	Reeves et al. (1983)
Caryophyllaceae			
<i>Arenaria humifusa</i>	W. Newfoundland	2330	Roberts (1992)
<i>A. marcescens</i>	W. Newfoundland	2365	Roberts (1992)
<i>A. rubella</i>	Skagit Co., Washington	1360	Kruckeberg et al. (1993)

L. (Reeves et al. 1983), three species of *Arenaria* (Roberts 1992; Kruckeberg et al. 1993) and two composites, *Senecio pauperulus* and *Solidago hispida* (Roberts 1992). Relevant data are summarized in Table 1.

The discovery of *Streptanthus polygaloides* as a hyperaccumulator occurred during a larger survey of California serpentine plants (Reeves et al. 1981), in which special attention was paid to *Streptanthus* because nearly all the twelve species in subgenus *Euclisia* are serpentine endemics (Kruckeberg and Morrison 1983). However, *S. polygaloides* was unique in the genus for its nickel-accumulating propensity, the concentrations being approximately 100 times greater than in the other serpentine species.

The initial study was based on the analysis of small samples of tissue taken from herbarium specimens, which has been useful as an exploratory tool in the investigation of nickel accumulation in other serpentine floras (Brooks et al. 1977). The present study was designed to extend the earlier work by obtaining and analyzing fresh field-collected samples of *Streptanthus* species together with soil samples from the same sites, and to investigate the behavior of various *Streptanthus* species grown under greenhouse conditions on

TABLE 2. LOCATION OF FIELD SPECIMENS OF *STREPTANTHUS* AND ASSOCIATED SOILS.
a Kruckeberg's field numbers.

Sam- ple no. ^a	Species	Location
6732	<i>S. polygaloides</i> A. Gray	Nevada Co., Washington Rd., 1.7 mi N of Route 20
6734	<i>S. polygaloides</i> A. Gray	Placer Co., S shore of Sugar Pine Reservoir, 8 mi E of Iowa Hill
6735	<i>S. polygaloides</i> A. Gray	Placer Co., 1.1 mi SW of Garden Valley
6736	<i>S. polygaloides</i> A. Gray	Calaveras Co., Route 49, 3 mi N of San Andreas
6737	<i>S. polygaloides</i> A. Gray	Tuolumne Co., Redhill Rd., 2.5 mi SW of Chinese Camp
6738	<i>S. polygaloides</i> A. Gray	Tuolumne Co., Route 49, 5.8 mi N of Coulterville
6739	<i>S. polygaloides</i> A. Gray	Mariposa Co., Route 49, 5.1 mi S of Coulterville
6740	<i>S. polygaloides</i> A. Gray	Mariposa Co., Route 49, 8.5 mi S of Coulterville
6741	<i>S. tortuosus</i> Kellogg	Mariposa Co., Route 49, 8.5 mi S of Coulterville
6742	<i>S. breweri</i> A. Gray	Napa Co., 0.5 mi on Berryessa-Knoxville Rd. from Route 128
6752	<i>S. breweri</i> A. Gray	Lake Co., Hill 1030, 4 mi NE of Middletown
6743	<i>S. hesperidis</i> Jepson	Lake Co., Rabbit Hill reserve, Middletown
6750	<i>S. hesperidis</i> Jepson	Lake Co., Hill 1030, 4 mi NE of Middletown
6744	<i>S. barbiger</i> E. Greene	Lake Co., Sulfur Cr. Rd.
6745	<i>S. barbiger</i> E. Greene	Lake Co., Sulfur Cr. Rd.
6746	<i>S. barbiger</i> E. Greene	Lake Co., S of junction, Routes 29 & 175
6748	<i>S. barbiger</i> E. Greene	Lake Co., Socrates Mine Rd.
6756	<i>S. barbiger</i> E. Greene	Mendocino Co., Feliz Cr. Rd., 0.8 mi W of Hopland
6757	<i>S. barbiger</i> E. Greene	Mendocino Co., Hopland-Yorkville Rd., 6.3 mi W of Hopland
6749	<i>S. morrisonii</i> F. W. Hoffm.	Napa Co., Butts Cr. Canyon, 1 mi E of county line
6751	<i>S. glandulosus</i> Hook.	Lake Co., Hill 1030, Middletown
6755	<i>S. glandulosus</i> Hook.	Mendocino Co., Mountain House Rd., 2.5 mi S of Hopland

serpentine and non-serpentine soils. We wished to probe such questions as the following: (i) do all populations of *S. polygaloides* exhibit nickel hyperaccumulation? (ii) do the nickel concentrations in field specimens of various *Streptanthus* species approximate those of the herbarium samples previously analyzed? (iii) how closely does the nickel-accumulating behavior under greenhouse conditions resemble that in the field? (iv) what happens to *S. polygaloides* when it is grown on non-serpentine soil?

Accordingly, in May 1988 we collected living plants from serpentine sites in the western foothills of the Sierra Nevada. Besides sampling eight populations of *S. polygaloides* there, we collected 14 other samples of 6 other *Streptanthus* species from serpentine sites in the Sierra Nevada and the Coast Ranges of California. Table 2 lists the locations and the taxa sampled.

Greenhouse experiments were carried out with seed of four species, *S. polygaloides*, *S. barbiger*, *S. insignis* and the non-serpentine *S. heterophyllus* Nutt., using four serpentine soils from California and Washington as well as a greenhouse compost soil.

MATERIALS AND METHODS

Field sampling. Three to five whole plants were harvested and stored in paper bags, and air-dried prior to analysis, which was carried out on the above-ground portion of the plants only. Herbarium voucher specimens (Kruckeberg 6732-6757) were also taken. A quick, semiquantitative test for nickel hyperaccumulation was made in the field by crushing leaf tissue onto a filter paper previously impregnated with a 1% ethanolic solution of dimethylglyoxime, which forms a red nickel complex, easily visible when the nickel concentration of the tissue is equivalent to more than 1000 µg/g on a dry weight basis. At each site a soil sample was taken from a depth of 2–10 cm; the soils were oven-dried, sieved to remove material >2 mm and then ground to –100 mesh (<150 µm) for analysis.

Greenhouse procedures. The origins of the seed and soils used in the greenhouse tests are summarized in Table 3. Seeds of each of the four species were sown, as a mixture, on the surface of each soil type; two 6" plastic pots were used for each soil type. Since the four species are readily distinguishable both as seedlings and as flowering plants, there was no difficulty in recognition. Pots were subirrigated regularly with distilled water. Germination rates were high for all taxa; no attempt was made to count the seedlings. In some cases crowding of seedlings may have inhibited their growth. Plants were harvested in three phases, described as young, intermediate and mature (approximately 4, 7 and 10 weeks, respectively, after germination). In the mature stage, plants of all taxa were in flower or in late bud. Samples of plants and soils were treated in the same way as the field samples prior to chemical analysis.

Chemical analysis. Plant tissue (pooled for each collection number) samples were weighed into borosilicate glass test tubes which were placed in a muffle furnace. The temperature was raised to 500°C over a 2-hour period and maintained at this level overnight. After cooling, the ash was dissolved in 2 M HCl and the solutions were analyzed for nickel by atomic absorption, using the spectral line at 232.0 nm. The volume of HCl used varied between 1.0 and 20.0

TABLE 3. SOILS AND *STREPTANTHUS* SEED USED IN GREENHOUSE TESTS.

Soil no.	Nature and origin
1	Serpentine, from chaparral, Hill 1030, 4 mi NE of Mid-dletown, Lake Co., CA
2	Serpentine, from barren talus, Newell Mine, King Cr., Chelan Co., WA
3	Serpentine, site with grasses/forbs, Newell Mine, King Cr., Chelan Co., WA
4	Dunite outcrop, Olivine Bridge, S Fork of Nooksack R., Skagit Co., WA
5	Greenhouse compost/loam, Univ. of Washington green-house
Seed species	Origin
<i>S. polygaloides</i>	Serpentine, 2.5 mi N of Bagby, Mariposa Co., CA
<i>S. barbiger</i>	Serpentine, hills above Cobb Valley, Glenbrook, Lake Co., CA
<i>S. insignis</i>	Serpentine talus, roadcut 6 mi W of Panoche Pass, San Benito Co., CA
<i>S. heterophyllus</i>	Granitic soil, disturbed chaparral, N of Escondido, San Diego Co., CA

ml, depending on the weight of sample taken and on the species. [Greater dilutions were used for *S. polygaloides* because of the higher nickel concentrations expected.] Several of these solutions were analyzed for a wide range of elements by inductively coupled plasma emission spectroscopy (ICP).

Soil samples (0.10–0.12 g) were digested in polypropylene beakers with 10 ml of 1:1 HF/HNO₃ mixture, evaporated to dryness and the residue taken up with 10 ml of 2 M HCl. After warming to assist dissolution, the solution volume was restored to 10.0 ml with deionized water. Samples of 2.0 ml were then diluted to 8.0 ml for analysis by ICP, this dilution being dictated by the need to keep the iron

TABLE 4. ANALYSES OF FIELD SAMPLES OF SERPENTINE *STREPTANTHUS* SPECIMENS. (Concentrations in µg/g unless otherwise indicated.) ^a No. of populations sampled in parentheses.

Species ^a	Element concentrations (dry weight basis)					
	Al	Ca (%)	Co	Cr	Cu	Fe
<i>S. polygaloides</i> (8)	81–412	0.58–2.10	21–83	2–59	3–11	91–1806
<i>S. tortuosus</i> (1)	43	0.72	5	8	4	130
<i>S. breweri</i> (2)	35–54	0.99–1.60	<1	1–2	3–4	78–121
<i>S. hesperidis</i> (2)	26–54	0.55–0.66	<1	1–2	4	71–92
<i>S. barbiger</i> (6)	24–85	0.29–1.39	<1–2	1–5	3–11	84–261
<i>S. morrisonii</i> (1)	19	0.92	1	2	2	98
<i>S. glandulosus</i> (2)	35–57	0.56–1.52	<1	2	3–7	139–260

concentrations below the 500 µg/ml level representing the upper limit of the ICP working range.

RESULTS

Field samples. The results for the ICP analyses of the field samples are shown in Tables 4 (plants) and 5 (soils). All eight population samples of *S. polygaloides* exhibited hyperaccumulation of nickel. Furthermore, in only two cases were the Ni concentrations below 10,000 µg/g (nos. 6738, 6740), and these corresponded to soils showing the least extreme chemical characteristics of serpentine, i.e., soils 6738 and 6740 had the lowest concentrations of Mg, Fe and Ni, and the highest concentrations of K, Na and Al, indicative of mixing with some non-ultramafic material. Nevertheless, even here, the soil Ni was still above 1000 µg/g, and the plant samples contained 7000 and 2430 µg/g Ni respectively.

All the other serpentine-endemic *Streptanthus* species contained only 4–22 µg/g Ni, values similar to, or lower than, those reported in the herbarium survey of Reeves et al. (1981).

The cobalt levels in *S. polygaloides* are also noteworthy. It is rare for plants, even on serpentines, to contain more than 5 µg/g of this element, although higher levels of Co (e.g., 10–200 µg/g) have occasionally been reported in Ni hyperaccumulators (Kersten et al. 1979; Kruckeberg et al. 1993).

With respect to the other elements shown in Table 4, there were no other major abnormalities, and no remarkable differences between *S. polygaloides* and the other species.

Greenhouse samples. The behavior of *S. polygaloides* as a nickel hyperaccumulator is strikingly confirmed. When grown on serpentine soils from sites where the species is not native, the plants consistently accumulated high levels of nickel (Table 5). When grown on a non-serpentine “background” soil (greenhouse potting mix), *S. polygaloides* plants had very low nickel levels (5–39 µg/g). All the

TABLE 4. EXTENDED.

Element concentrations (dry weight basis)							
K (%)	Mg (%)	Mn	Na	Ni	P	Zn	
1.27–2.72	0.57–1.30	44–225	658–1476	2430–18,600	1760–4420	17–95	
1.20	1.13	146	665	12	2450	48	
1.77–2.68	1.58–2.30	69–106	520–566	7–13	3440–4510	27–32	
0.88–1.06	2.15–2.25	55–67	303–401	19–22	3750–11,790	78–110	
0.86–1.75	1.39–3.74	52–207	194–602	4–21	1680–5510	13–93	
0.67	1.43	101	300	5	1040	29	
1.22–1.74	0.94–1.27	24–28	661–737	10–12	2140–2410	13–39	

TABLE 5. ANALYSIS OF SOILS AT *STREPTANTHUS* SITES ON SERPENTINE (n = 22). (Concentrations in $\mu\text{g/g}$ unless otherwise indicated.)

Element	Concentration		
	Lowest	Median	Highest
Al (%)	0.25	1.38	5.46
Ca (%)	0.072	0.426	1.95
Co	85	178	350
Cr	549	1420	3430
Cu	30	45	274
Fe (%)	5.16	9.10	13.8
K (%)	0.026	0.084	0.944
Mg (%)	4.40	15.14	21.25
Mn	711	1304	3420
Na	259	662	8620
Ni	1060	3030	4620
P	115	280	1080
Zn	68	109	265

serpentine soils bioassayed for nickel with *S. polygaloides* had substantial nickel concentrations ($> 1000 \mu\text{g/g}$); the "background" non-serpentine soil had only $52 \mu\text{g/g}$ nickel (Table 6).

Plants of *Streptanthus insignis* from a serpentine locality in the inner South Coast Ranges of California, failed to accumulate significant amounts of nickel when grown on the three serpentine test soils. Nickel values for this serpentine endemic ranged from 15 to $186 \mu\text{g/g}$. This finding substantiates the low nickel values from herbarium samples (Reeves et al. 1981). The other serpentine endemic, *S. barbiger* of the North Coast Ranges, varied widely in its nickel accumulation (Table 7). On one serpentine soil (Newell Mine from Washington State), plants accumulated as much as $1200 \mu\text{g/g}$, and could be classed as a hyperaccumulator species. Yet nickel values ranged from only 69 to $850 \mu\text{g/g}$ on other serpentine test soils. Nickel values from herbarium samples of this species in the 1981 report were even lower ($22\text{--}27 \mu\text{g/g}$). Similar low values were obtained from field-collected *S. barbiger* in 1988 ($4\text{--}21 \mu\text{g/g}$, Table 4). These puzzling results, suggesting incipient capacity for hyperaccumulation by this species, merit further consideration in the Discussion section.

Nickel levels in *S. polygaloides* grown on greenhouse potting mix ($5\text{--}39 \mu\text{g/g}$) can be traced to the storage of nickel in the seed collected on native serpentine soil. The one *Streptanthus* from a non-serpentine habitat, *S. heterophyllus*, failed to grow sufficiently on serpentine for use in chemical analysis.

DISCUSSION

Streptanthus polygaloides. Nearly all tissue samples of *S. polygaloides* proved to have hyperaccumulator levels for nickel (> 1000

TABLE 6. ELEMENT CONCENTRATIONS IN SOILS USED IN GREENHOUSE TESTS. (Concentrations in $\mu\text{g/g}$ unless otherwise indicated.)^a See Table 3 for further details.

Soil ^a	Al (%)	Ca (%)	Co	Cr	Cu	Fe (%)	K (%)	Mg (%)	Mn	Na (%)	Ni	P	Zn
1. Serpentine, Hill 1030	0.70	0.224	200	426	30	11.3	0.106	17.9	1610	0.230	3690	617	215
2. Serpentine, talus, Newell Mine	1.58	0.683	118	684	30	5.59	0.100	19.4	1060	0.537	1810	209	93
3. Serpentine, grassland, Newell Mine	3.77	2.300	90	571	25	4.95	0.262	11.4	1070	0.999	1130	481	90
4. Serpentine, Olivine Bridge	0.41	0.259	163	178	19	6.75	<0.022	22.4	1020	0.114	2880	158	96
5. Greenhouse compost/loam	5.29	2.480	19	81	53	2.47	0.673	0.87	636	1.790	52	1940	262

TABLE 7. NICKEL CONCENTRATIONS ($\mu\text{g/g}$) IN *STREPTANTHUS* PLANTS GROWN ON VARIOUS SOILS. ^a *S. heterophyllus* seedlings did not survive on serpentine soils. ^b Maximum value found in herbarium or field specimens (Reeves et al. 1981 and this work).

Soil	Species			
	<i>S. polygaloides</i>	<i>S. barbiger</i>	<i>S. insignis</i>	<i>S. heterophyllus</i> ^a
1. Serpentine, Hill 1030	2110–5460	69–850	55–105	—
2. Serpentine, talus, Newell	1480–2120	550–1200	26–186	—
3. Serpentine, grass, Newell	660–4200	106–456	15–38	—
4. Serpentine, Olivine Bridge	1560–4960	766	18–59	—
5. Greenhouse	5–39	17	3–6	6–7
Field specimens, max. ^b	18,600	27	83	<10

$\mu\text{g/g}$), whether taken from native field sites or when grown in the greenhouse on serpentine soils from localities where *S. polygaloides* is not native. It was not surprising that the one sample of stem tissue (Table 7) contained 660 $\mu\text{g/g}$ of nickel; stems have higher proportions of structural components (cell wall material) and are generally found to have lower nickel concentrations, even in the hyperaccumulator species.

This species, grown on a variety of serpentine soils in the greenhouse had somewhat lower concentrations of nickel (max. of 5460 $\mu\text{g/g}$) than did the field-collected samples. This difference may be a function of differences in plant age and/or mode of growth. In the field, the plants behave as winter annuals, growing as rosettes in the fall and winter, until they bolt in the following spring. During that long growth period, plants in the field can accumulate nickel more or less continuously and thus reach higher concentrations. In contrast, greenhouse plants grow rapidly to maturity in ca. 10 weeks, with less time for nickel uptake. Also greenhouse cultures are afforded optimal conditions for growth (consistent watering, favorable temperatures, etc.).

Other species of Streptanthus. None of the other field-collected serpentine taxa were hyperaccumulators. This was true also for greenhouse-grown *S. insignis*. This confirms the conclusion of Reeves et al. (1981), for results from herbarium samples: Of the several serpentine species of *Streptanthus*, only *S. polygaloides* is a hyperaccumulator of nickel. The one non-serpentine species, *S. heterophyllus*, failed to survive on any serpentine soil. It showed complete intolerance to serpentine conditions, including the high nickel levels.

Streptanthus barbiger. This species grown in the greenhouse on several non-native serpentine soils showed moderate levels of nickel

accumulation, even exceeding 1000 $\mu\text{g/g}$ in one sample (Table 7). *S. barbiger* in the field samples had only low levels of nickel (4-21 $\mu\text{g/g}$, Table 4), and thus acts in the field like a nickel excluder. This surprising result on non-native soils raises the possibility that *S. barbiger* possesses an incipient ability for hyperaccumulation, which may be triggered when grown on non-native serpentine soils, or as well, when growing under greenhouse conditions. This result is all the more curious since *S. insignis*, another serpentine endemic, when grown under similar conditions, does not show any sign of incipient hyperaccumulation.

Although nickel hyperaccumulation is primarily a property of a limited range of serpentine plant species, the degree to which nickel is excluded by normally "non-accumulating" species can sometimes be significantly modified by changes in external conditions, especially soil and climate. Thus a change to another soil (still of ultramafic origin and overall comparable elemental composition) and/or different growth conditions (as in a greenhouse) may provide enough change in factors such as soil pH, Ni availability, soil texture and moisture retention, soil mycorrhizae and diurnal temperature variation, as to lead to considerably increased nickel uptake in some species.

Streptanthus barbiger appears to be an ideal subject for further detailed studies of nickel accumulation. Our research with plants in the field and with plants grown on non-native serpentines, suggests an inherited preadaptation for nickel uptake. It could be that *S. barbiger* has a genetically acquired capacity for nickel uptake, yet has not reached the evolved status of a full-blown hyperaccumulator. A number of approaches present themselves: 1. It may be possible to select for increased nickel accumulation on native or non-native serpentine soils. Individuals with higher nickel levels could be selfed for further selectional response to nickel. 2. Crosses between individuals (intrapopulation or interpopulation) with incipient accumulation capacity could enhance the uptake ability of the progeny. 3. More accessions of population samples of *S. barbiger* could be grown on native and non-native serpentine soils and tested for nickel levels. These trials could be done for plants from both greenhouse culture and plants in the field. In the latter venue, seed of *S. barbiger* could be sown in the field on several serpentine sites where the species is not native. This regime might confirm the potential of *S. barbiger* for nickel accumulation from some serpentine soils, or might indicate that the climatic conditions of the greenhouse are largely responsible for the anomalous behavior observed here.

Evolutionary considerations. We are not unmindful of the evolutionary implications of these results. The most obvious question is why some few serpentine endemics are hyperaccumulators and

others are not; yet still another, *S. barbiger*, may be an incipient accumulator. The related question, equally intriguing, is why most serpentine plants are NOT hyperaccumulators (e.g., exclude nickel).

As a working hypotheses, we propose the following: 1. The nature of the mechanism of hyperaccumulation is idiosyncratic. Each hyperaccumulator, or group of taxonomically related hyperaccumulators can have evolved its own mechanisms for nickel uptake. This seems likely since nickel accumulation occurs in many different and unrelated plants and in many different serpentine environments, tropical to temperate. 2. There may be some degree of genetic preadaptation for nickel accumulation in serpentine tolerant species, as suggested by our findings for *S. barbiger*. Indeed, the early stages of achieving high nickel uptake are likely to involve genotypes preadapted to a modest capability for nickel uptake. One of us (Kruckeberg 1986) has elaborated on the evolutionary sequence for serpentine tolerance by acquiring early, partial preadaptation. The same sequence could apply to the acquisition of a hyperaccumulator genotype.

The most unresolved questions have to do with the evolutionary development of a cellular and molecular basis for nickel accumulation—and for serpentine tolerance in general. What physiological and molecular mechanisms account for this remarkable edaphic capacity? A combination of physiological and molecular biological techniques are needed to solve the fundamental question: How and why does a plant do what it does on serpentine? Alan Baker (1987) has put the research potential well: ". . . metal tolerance [and metal accumulation] in plants will continue to intrigue all those plant scientists attempting to understand the nature and scale of plant adaptations to the environment and will remain an evolutionary paradigm par excellence."

ACKNOWLEDGMENTS

We acknowledge the assistance of Dr. J. Lee, AgResearch Grasslands, Palmerston North, in providing access to the ICP for some of the analyses.

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ANNOUNCEMENT

NEW PUBLICATION

O'LEARY, J. F., S. A. DESIMONE, D. D. MURPHY, P. F. BRUSSARD, M. S. GILPIN, and R. F. NOSS. 1994. *Bibliographies on Coastal Sage Scrub and Related Malacophyllous Shrublands of Other Mediterranean-Type Climates*. California Wildlife Conservation Bulletin No. 10. 51 p. Contents: Bibliographic sets on various aspects of coastal sage scrub shrublands (e.g., animals; conservation, restoration, and management; fire, diversity, and succession; maps; morphology, phenology, and physiology; soils and water resources; etc.). This is a comprehensive collection of bibliographies regarding an imperiled vegetation type. Copies may be obtained *gratis* from: Kathie Vouchillas, California Department of Fish and Game; 1416 Ninth Street; Sacramento, CA 95814 (916-324-3814) or call California Department of Fish and Game office in San Diego (619-467-4251).

WOODY VEGETATION AND SUCCESSION IN THE GARIN WOODS, HAYWARD HILLS, ALAMEDA COUNTY, CALIFORNIA

HUGH DEFOREST SAFFORD¹

Department of Biological Sciences, California State University,
Hayward, CA 94542

ABSTRACT

Floral composition, stand structure, and successional relationships were studied in a stand of broadleaf evergreen forest in the East San Francisco Bay Hills, Hayward, Alameda County, California. Data from this study furnishes the first detailed profile of the woody plant communities in the Hayward Hills and provides a model for comparisons with other East Bay woodlands. Three main vegetational types were identified and characterized: a lower, bay (*Umbellularia californica*) woodland/forest; an upper, oak (*Quercus agrifolia*) woodland; and a central, apparently transitional oak-bay woodland; each vegetation type is defined by a distinctive tree-shrub assemblage. The author found good evidence to support McBride's (1974) paradigm of East Bay plant succession, i.e., a general movement toward a bay-dominated community and away from an oak-dominated assemblage. On the study site tree-fall of dead madrone (*Arbutus menziesii*) has opened much of the canopy and may be affecting the rate of this successional pattern.

Mixed evergreen forest is the dominant vegetation type in the hills of the eastern San Francisco Bay Area (Kuechler 1977; Sawyer *et al.* 1988). In central-coastal California north of Monterey County, this association includes *Pseudotsuga menziesii* (Douglas-fir), *Lithocarpus densiflora* (tan oak), *Quercus chryssolepis* (canyon live oak), *Aesculus californica* (buckeye), *Umbellularia californica* (bay), *Arbutus menziesii* (madrone), *Acer macrophyllum* (big-leaf maple), and *Quercus agrifolia* (coast live oak) (Munz and Keck 1959). In the East San Francisco Bay Hills, Douglas-fir and tan oak are absent (Havlik 1974); in this area the less general epithet 'broadleaf evergreen forest' is often employed (Smith 1960).

On the eastern margins of the San Francisco Bay Area, broadleaf evergreen forest stands are dominated by two species, *Quercus agrifolia*, and *Umbellularia californica*. In a study of floral community succession in the Berkeley Hills, McBride (1974) found evidence that *Q. agrifolia*-dominated oak woodland represents the climax community in areas where grazing is light and ground fires occur periodically. Given these conditions, grasses give way to *Baccharis pilularis* and associated shrubs, and these in turn are replaced by a

¹ Present address: Graduate Group in Ecology, University of California, Davis, CA 95616.

coast live oak-dominated assemblage. In heavily grazed stands that are protected from fire, this oak woodland is succeeded by *U. californica*-dominated "bay woodland". Intermediate conditions favor the existence of a mixed "oak-bay woodland". In general, McBride found that modern East Bay conditions favored development of bay woodland and forest at the expense of oak-dominated communities. In this paper, woodland is defined as a tree-dominated community (>30% tree cover) with an open canopy; forest has a closed canopy.

General, qualitative descriptions of oak- and bay woodland and mixed broadleaf forest are available in Cooper (1922), Bowerman (1944), Munz and Keck (1959), McBride (1974), Griffin (1988) and Sawyer et al. (1988) etc., but few quantitative data have been published on the floristic composition, stand structure and successional trends of these vegetation types in the East San Francisco Bay Area (an exception is Wetzel (1972)). The lack of basic ecological research in the Hayward Hills was the primary motivation for the initiation of this study.

This research, conducted between January and May of 1994, sought: (1) to identify the major floristic components and stand structure of the woody plant communities in Garin Woods, a broadleaf evergreen forest and woodland in the Hayward Hills, Alameda County; and (2) to shed some light on the possible successional relationships between these communities.

Study site. The study was located at the Garin Woods ecology field station of the California State University, Hayward, Alameda County, California, approximately one kilometer southeast of the C.S.U. campus, and 10 km east of the San Francisco Bay (lat. 37°39', long. 122°2'30") (Fig. 1). Topography is hilly and locally very steep; elevations within the station property range from approximately 110 m in the Zeile Creek drainage on the west, to about 240 m on hilltops on both the north and south boundaries. The study site itself is on a north-facing slope of 35 to 45+ degrees declivity and contains approximately 7.1 hectares of broadleaf evergreen woodland and forest, and some scrubland. Grassland frames the site on both south and west.

Local geology is complex and poorly understood. Geologic mapping on land immediately adjacent to the Garin Woods field station has uncovered a complicated medley of gabbro and serpentine, ocean sediments and metamorphic rocks, and mudstones with interbedded sandstones and limestone nodules; local hilltops (and most of the study site) are the Quaternary Leona Rhyolite (Robinson 1956; Dibblee 1980).

The Garin Woods are located wholly within the Altamont-Diablo soil association, which is composed of moderately sloping to very steep, brownish and dark-gray, moderately deep soils; parent ma-

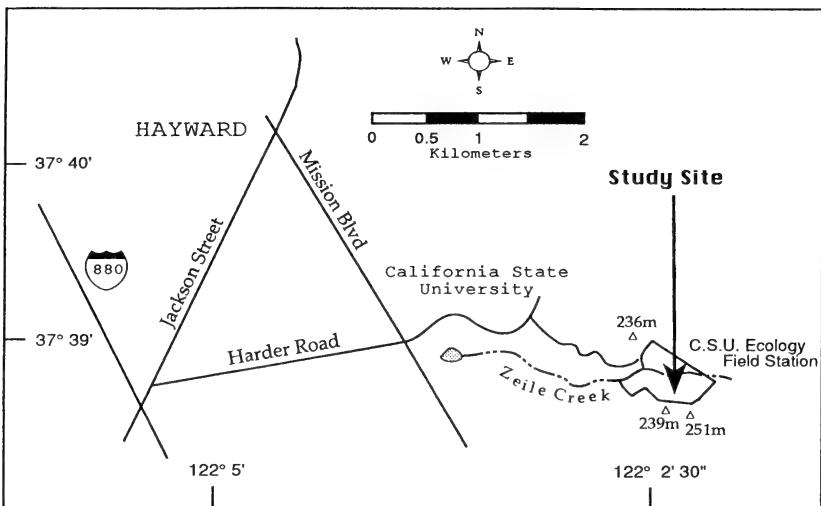


FIG. 1. Study site location. The site itself is located on a north-facing slope south of Zeile Creek (arrow).

terial is primarily soft sedimentary rock. The study site itself is found almost entirely on the Los Gatos-Los Osos Complex of loam and silty clay loam. Woodland edges and surrounding grassland are on the Altamont rocky clay, a moderately deep soil found on more shallowly sloped (7–30%), mostly south-facing slopes (Soil Conservation Service 1966).

Local climate is mediterranean, with cool, humid winters and warm, dry summers. Climatic data for the study site is unavailable, but extrapolation from regional isotherm maps yields a mean annual temperature of approximately 14.5°C, a maximum monthly mean of 24°C in July and a minimum monthly mean of 4°C in January. Annual precipitation averages approximately 545 mm, with 85% falling between November and April. Winds are predominantly from the north west and the west (A.B.A.G. 1974).

The study site, privately owned prior to its sale to the university, has been protected from fire for most of the last century. Intermittent livestock grazing occurred on the property until approximately 15 years ago. Cattle grazing continues south of the study site in Garin/Dry Creek Pioneer Regional Park. Fences separating the two properties are in poor condition and minor incursions of livestock onto university property occur from time to time. The present intensity of deer grazing is difficult to establish; the author's observations suggest that at least a half-dozen mule deer (*Odocoileus hemionus*) regularly feed in the area, and that browsing is locally heavy.

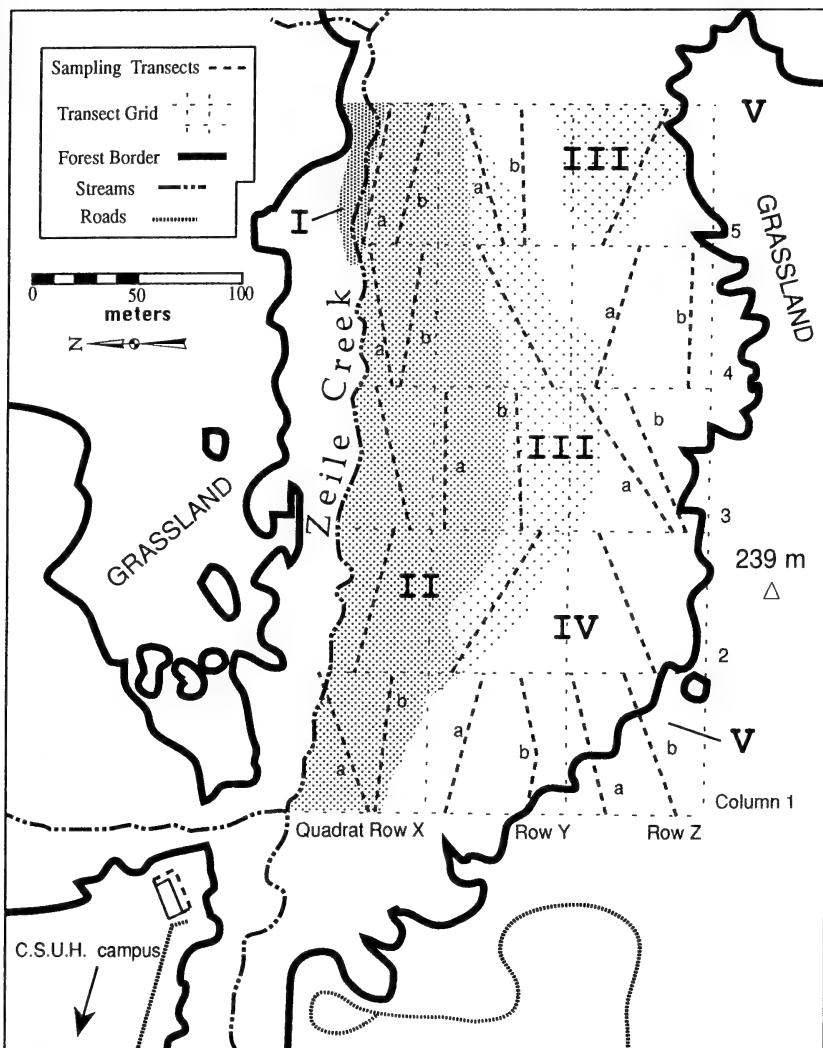


FIG. 2. Study site, with sampling quadrats (transect grid) and transect locations, and approximate boundaries of the woody vegetation types discussed in this paper. I) riparian woodland; II) bay woodland; III) oak-bay woodland; IV) oak woodland; V) *Artemisia*-grassland scrub.

MATERIALS AND METHODS

Data collection. The forest vegetation was sampled along 24 transects between January and April, 1994, using the point-centered quarter method (Cottam and Curtis 1956). In this method, random points are chosen along a transect, the area around each point is

divided into four 90 degree quarters, and the nearest tree (or shrub) in each quarter is sampled.

Preliminary field reconnaissance suggested the existence of three fairly distinct woody plant assemblages grading from the base of the hill to near the summit, therefore a stratified-random sampling scheme was employed to maximize sampling precision. Transect placement was determined using a grid of 15 75 m × 75 m quadrats (3 north-south × 5 east-west) overlaid on the U.S.G.S. 7.5-minute Hayward Quadrangle map (Fig. 2). Nine quadrats to be sampled were randomly chosen, three from each of the three north-south quadrat-rows. Two sampling transects were placed on the map in each chosen quadrat by randomly choosing two points (figured in meter distances) along the east and west sides of each selected quadrat, and then connecting the northernmost points on east and west to form transect 1; transect 2 was drawn between the southern points. A preliminary estimate of sample size requirement was made using Seber's formula for plotless sampling methods (Krebs 1989).

When half of all planned transects had been run, distance data were analyzed for distributional pattern using POISSON and NEG-BINOM (Krebs 1989). This analysis showed that the vegetative pattern was aggregated ($k = 10.08144$, standardized Morisita Coefficient = 0.5001). Taking this aggregation into account, an updated computation of sample size requirement was made using SAMPLE (Krebs 1989), and necessitated one additional sampling transect within each vegetative type. Since there were two unsampled quadrats remaining in each quadrat-row, I decided to run one extra transect in each, so as to maximize coverage of the study site. Ideally, two transects would have been sampled in all of the quadrats, but time constraints did not permit this.

Point-centered quarter transect lines were coursed using the field map, compass triangulation and paced measurements. At randomly chosen intervals (at least seven meters apart to avoid sampling the same plant twice) distance was measured, height estimated, and species type noted, for the nearest canopy member (defined as any woody plant ≥ 2 meters in height receiving direct, overhead sunlight) and the nearest 'middle story' member (defined as woody plants ≥ 2 meters in height not comprising part of the canopy, i.e., existing in the shade of a larger neighbor) in each 90° quarter. Every transect included at least seven sampling points.

Diameter at breast height (dbh) measurements were not taken in the initial survey—the author was originally interested only in species diversity and floristic composition—but the obvious effects of local madrone mortality and competition between both canopy and middle story species on present stand composition and structure underlined the importance of this data to any interpretation of the present situation in the Garin Woods. Therefore, in May, 1994, four additional point-quarter transects were sampled, across the study

site from east to west, to measure dbh of the canopy tree species. The transects were regularly spaced so as to maximize coverage of each of the vegetation types. One dbh measurement was made of the nearest specimen of each canopy species in every quarter, except in the case of *Arbutus menziesii*, where every specimen sighted (dead or alive, standing or fallen) was measured for dbh.

Data analysis. Point-quarter data from 24 transects were compiled and analyzed for mean point-to-plant distance, relative densities (percentage of sampled stand), and total density using QUARTER (Krebs 1989).

Indices of dispersion were calculated by dividing the variance of point-to-nearest neighbor distances for each vegetation type by the mean point-to-nearest neighbor distance ($\text{var.}/\bar{x}$).

Vegetation types and plant community relationships were noted in the field and clarified by tabling and plotting relative density data. Key inter- and intracommunity relationships were identified and correlated using REGRESS (Krebs 1989). Using these indicator relationships, the proportions of *U. californica* vs. *Q. agrifolia* in the canopy, and field observations, each transect was assigned to one of three vegetation types: bay woodland and forest, oak-bay woodland, or oak woodland.

Size-frequency data were compiled and plotted to provide further evidence for climax vegetation types and successional relationships between the species of the Garin Woods canopy.

Species nomenclature follows Hickman (1993).

RESULTS

Woody plant communities. Field experience and the data collected through point-quarter sampling elucidated five major woody plant communities on the study site: bay woodland and forest, oak-bay woodland, oak woodland, riparian woodland, and *Artemesia*-grassland scrub. This study was directly concerned with the three broadleaf evergreen communities but some transect lines crossed riparian woodland and *Artemesia*-grassland scrub as well. Table 1 outlines the characteristic floral components of the five woody vegetation types.

Stand structure. Data from the 24 point-quarter transects are shown in Table 2, and in Figure 3. Assignment of transects to the three broadleaf vegetation types was made using the following criteria:

- 1) Relative proportions of *U. californica* vs. *Q. agrifolia* in the canopy.
- 2) Floristic composition and stand structure of the middle story (see below).
- 3) Field observations.

TABLE 1. WOODY VEGETATION TYPES IN THE MAIN GARIN WOODS, C. S. U. H. RESEARCH FOUNDATION ECOLOGY FIELD STATION, HAYWARD HILLS, ALAMEDA COUNTY, CALIFORNIA.

Vegetation type	Site description	Area	Dominant species	Associated species
Riparian Woodland	Streambank and alluvial terraces, NE corner	0.1 ha	<i>Salix lasiolepis</i> <i>Salix laevigata</i> <i>Acer macrophyllum</i>	<i>Prunus virginiana</i> <i>Cornus sericea</i> ssp. <i>sericea</i> <i>Baccharis pilularis</i> <i>Heteromeles arbutifolia</i> <i>Corylus cornuta</i> var. <i>californica</i> <i>Quercus agrifolia</i> <i>Arbutus menziesii</i> <i>Acer macrophyllum</i>
Bay Woodland/Forest	Steep slopes (40–50 deg.) on lower hillside, N facing	2.8 ha	<i>Umbellularia californica</i>	<i>Toxicodendron diversilobum</i> <i>Holodiscus discolor</i> <i>Heteromeles arbutifolia</i> <i>Arbutus menziesii</i> <i>Garrya elliptica</i>
Oak-Bay Woodland	Moderately sloped, discontinuous along center of hill, N facing	1.4 ha	<i>Quercus agrifolia</i> <i>Umbellularia californica</i>	<i>Toxicodendron diversilobum</i> <i>Umbellularia californica</i> <i>Holodiscus discolor</i> <i>Ribes</i> spp.
Oak Woodland	Moderately to shallowly sloping, upper hillside to ca. 230 m, N facing	2.9 ha	<i>Quercus agrifolia</i>	<i>Quercus garryana</i> × <i>durata</i> <i>Quercus durata</i> <i>Rhamnus crocea</i> <i>Mimulus aurantiacus</i>
(Oak Woodland–Grassland Ecotone)	0–25 m wide, bordering Oak Woodland on SW, mostly W facing	—	Stunted <i>Q. agrifolia</i> and <i>U. californica</i>	<i>Quercus palmeri</i>
Artemisia–Grassland–Scrub	W and S edges of study site	0.2 ha	<i>Artemisia californica</i>	<i>Lupinus albifrons</i> var. <i>collinus</i> Various perennial grasses

TABLE 2. QUANTITATIVE DATA FOR WOODY PLANTS OF THE CANOPY AND MIDDLE STORY IN THE GARIN WOODS. Species observed but not sampled are indicated by (x). For transect location see Figure 2.

Transects	Bay woodland X1a, X1b, X2, X3, X4a, X4b, X5a, X5b, Y3a	Oak-Bay woodland Y2, Y3b, Y4, Y5a, Z5	Oak woodland Y1a, Y1b, Y5b, Z1, Z2, Z3a, Z3b, Z4a, Z4b	Study site totals
Approximate sampled area (hectares)	2.8	1.4	2.9	7.1
Canopy				
Total sample size	177	95	155	427
Index of dispersion (var./ \bar{x})	1.80	1.52	1.31	
Density (/hectare)	247.6	300.4	369.9	
Density 95% C.L.	213.3–286.7	244.9–366.9	315.4–432.6	
Relative density of canopy species (%)				
<i>Acer macrophyllum</i>	2.9	1.1	0.0	1.4
<i>Alnus rhombifolia</i>	0.6	0.0	0.0	0.2
<i>Arbutus menziesii</i>	8.5	7.4	0.0	5.2
<i>Garrya elliptica</i>	0.0	0.0	1.9	0.7
<i>Heteromeles arbutifolia</i>	0.0	0.0	0.7	0.2
<i>Prunus virginiana</i>	0.6	0.0	0.0	0.2
<i>Quercus agrifolia</i>	15.3	48.4	69.0	42.1
<i>Quercus chrysolepis</i>	x	0	0	—
<i>Quercus palmeri</i>	0.0	2.1	0.0	0.5
<i>Quercus garryana</i>				
<i> x durata</i>	0.0	0.0	5.8	2.1
<i>Salix lasiolepis</i>	0.6	0.0	0.0	0.2
<i>Umbellularia californica</i>	71.2	41.1	22.6	46.9
Middle story				
Total sample size	178	95	154	427
Index of dispersion (var./ \bar{x})	2.00	0.70	1.44	
Density (/hectare)	381.7	1173.4	855.9	
Density 95% C.L.	326.1–445.4	956.6–1432.9	729.5–1001.4	
Relative density of middle story species (%)				
<i>Acer macrophyllum</i>	1.7	0.0	0.0	0.7
<i>Artemisia californica</i>	0.0	0.0	0.7	0.3
<i>Baccharis pilularis</i>	0.0	1.1	0.7	0.5
<i>Cercocarpus betuloides</i>	0.0	0.0	0.7	0.3
<i>Cornus sericea</i> var. <i>sericea</i>	1.1	0.0	0.0	0.5
<i>Corylus cornuta</i>	13.5	4.2	x	6.6
<i>Garrya elliptica</i>	0.6	6.3	1.3	2.1
<i>Heteromeles arbutifolia</i>	34.3	11.6	4.6	18.5
<i>Holodiscus discolor</i>	4.5	15.8	13.6	10.3
<i>Mimulus aurantiacus</i>	0.0	1.1	1.3	0.7

TABLE 2. Continued.

Transects	Bay woodland X1a, X1b, X2, X3, X4a, X4b, X5a, X5b, Y3a	Oak-Bay woodland Y2, Y3b, Y4, Y5a, Z5	Oak woodland Y1a, Y1b, Y5b, Z1, Z2, Z3a, Z3b, Z4a, Z4b	Study site totals
<i>Oemleria cerasiformis</i>	x	1.1	1.3	0.7
<i>Quercus agrifolia</i>	5.0	1.1	5.8	4.4
<i>Quercus durata</i>	0.0	0.0	1.3	0.5
<i>Quercus palmeri</i>	0.0	2.1	x	0.5
<i>Rhamnus californica</i>	1.1	x	1.3	0.9
<i>Rhamnus crocea</i>	0.0	0.0	0.7	0.2
<i>Ribes</i> spp.	x	1.1	5.2	2.1
<i>Sambucus mexicana</i>	x	x	x	—
<i>Toxicodendron diversilobum</i>	5.0	26.3	44.8	24.1
<i>Umbellularia californica</i>	33.1	28.4	16.2	26.0

Criterion 2 involved a series of comparisons. In the Garin Woods *Toxicodendron diversilobum* (as a shrub ≥ 2 m) exhibits a very low affinity for stands dominated by *U. californica*. Correlation of data combined from all three vegetation types showed that this negative relationship is statistically significant (Fig. 4a), and it was thus taken as a fairly reliable measure of the vegetation type. (Pooling data from three different sampling strata raises valid questions regarding the statistical independence of those data points found within each respective stratum: in this paper, Figures 4a and 4b are employed only to illustrate an important ecological reality—for my present purposes the causes of this reality are immaterial.)

Other members of the middle story were also found to exhibit important vegetation-type affinities, for whatever reason: *Heteromeles arbutifolia* is the most common middle story member in bay woodland/forest, but it was not sampled on any of the transects from transect-row Z (except for Z5), which is primarily oak woodland (see Fig. 4b); *Corylus cornuta* showed a similar pattern. *Holodiscus discolor* occurred most commonly along the middle of the hill, under the often open canopy of the oak-bay woodland. Middle story density (individuals/hectare), and indices of dispersion for both the canopy and middle story were also considered meaningful gauges of vegetation type.

Succession. Data from the diameter-breast-height (dbh) measurements for Garin Woods as a whole are shown in Figure 5. *U. californica* shows the reverse J curve considered indicative of climax species (note the variation in the 21–25 cm size-class however). Figure 3b portrays the relative density of *U. californica* within the

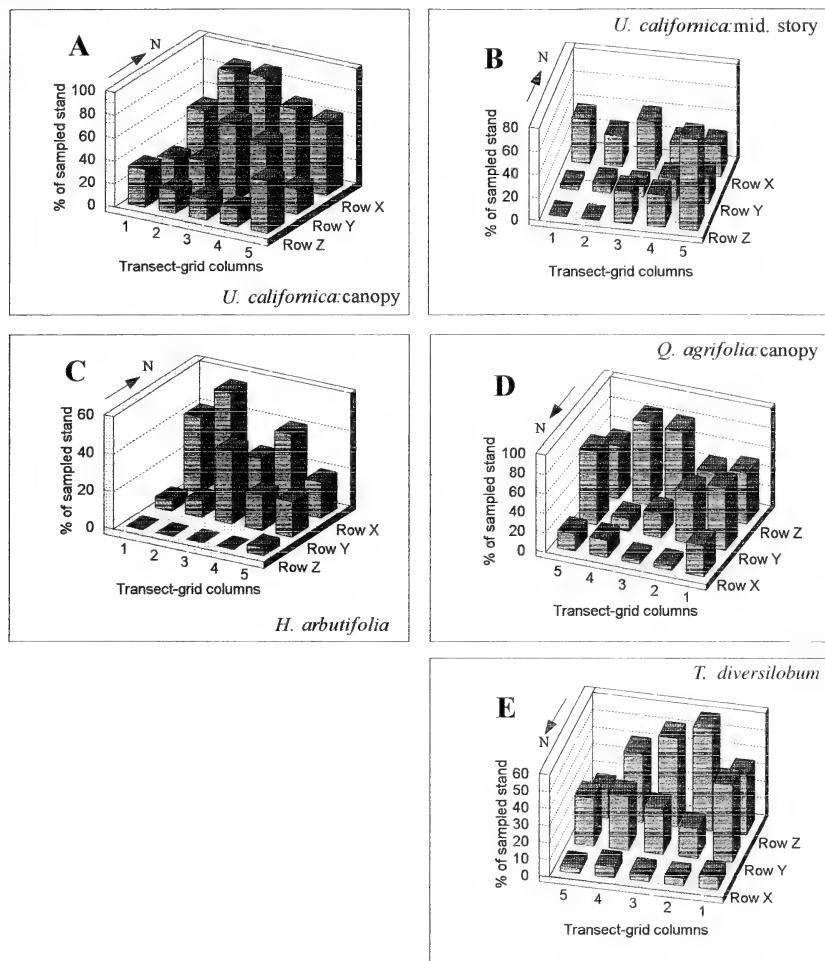


FIG. 3. Three-dimensional histograms of the distributions of selected woody species on the study site. Columns and Rows correspond to the quadrats in Figure 2. Each bar represents an approximation, derived from either one or two sampling transects (see Figure 2), of the relative frequency of each species in each quadrat. Note that Figures 3A through C are oriented 180° from Figures 3D and E. A) *Umbellularia californica*: canopy; B) *U. californica*: middle story; C) *Heteromeles arbutifolia*; D) *Quercus agrifolia*: canopy; E) *Toxicodendron diversilobum*.

middle story of each quadrat, i.e., the relative numbers of saplings and small trees within each stand. Taken together, Figures 3a, 3b and 5 point to the existence of different stands in various stages of successional progression within the Garin Woods; some are obviously older stands, with relatively little recruitment of *U. californica*

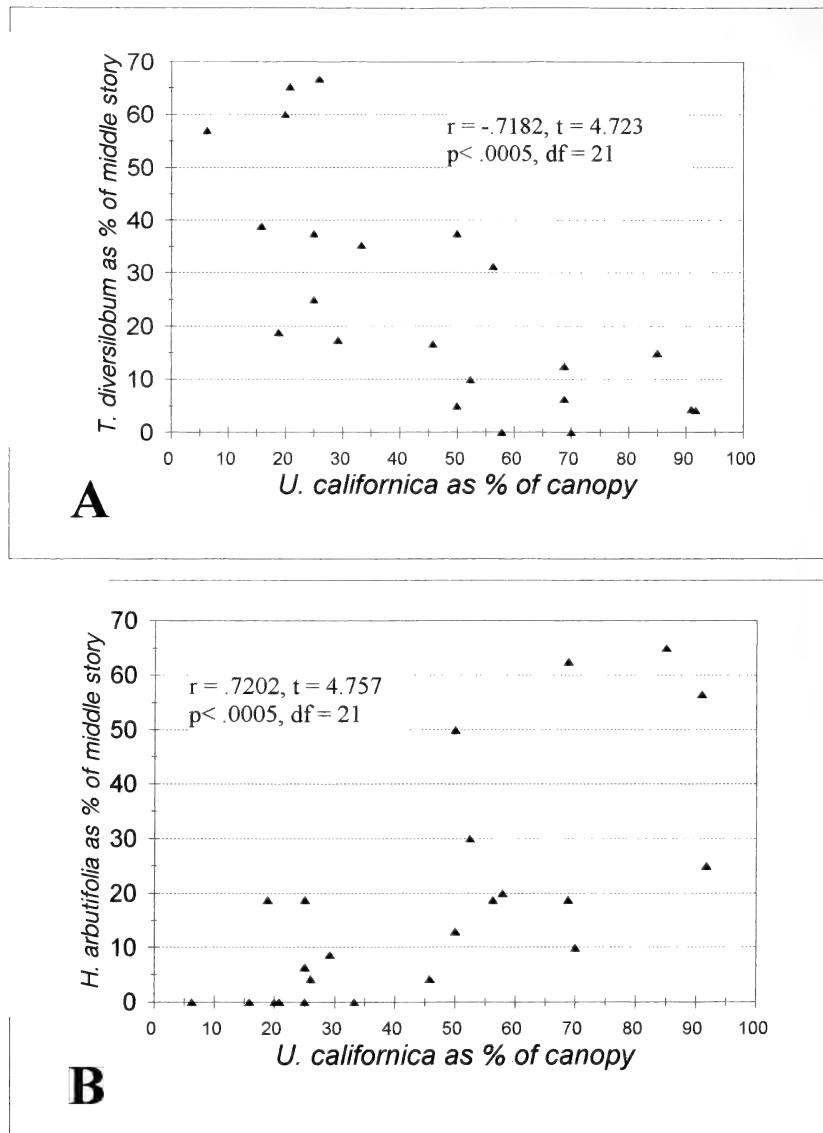


FIG. 4. A) Correlation of *Toxicodendron diversilobum* as a component of the middle story versus *Umbellularia californica* as a component of the canopy; B) Correlation of *Heteromeles arbutifolia* as a component of the middle story versus *U. californica* as a component of the canopy.

(Y3), while others (Z5) have fewer mature individuals and abundant recruitment; a few stands (X2, X3) seem to have ample recruitment even though their canopies are already $>90\%$ *U. californica*.

Figure 5 also shows size-frequency data for *Q. agrifolia* and *A.*

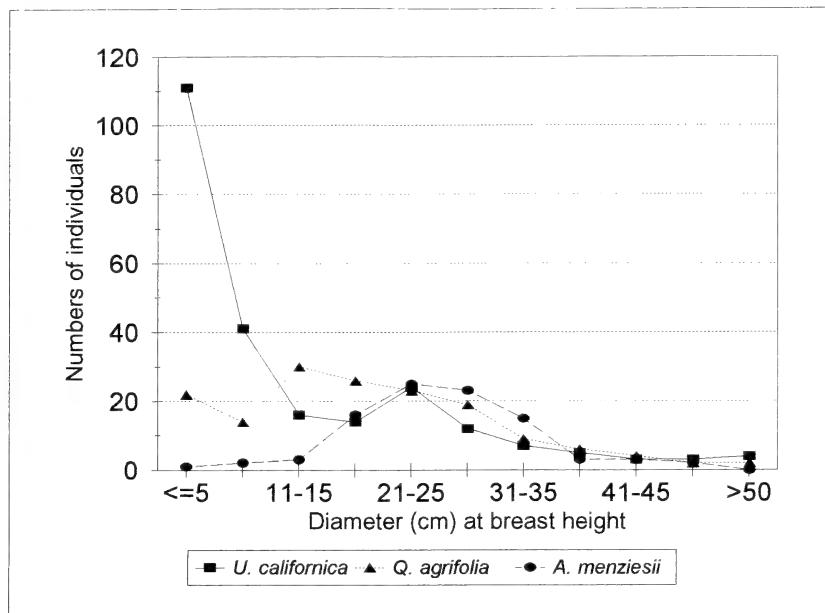


FIG. 5. Size-class data for *Umbellularia californica*, *Quercus agrifolia* and *Arbutus menziesii* in the Garin Woods. Both live and dead specimens of *A. menziesii* are included.

menziesii. There is little recruitment of *Q. agrifolia* in the Garin Woods. In fact, of the 22 measured individuals ≤ 5 cm in diameter, 9 occurred along a man-made trail in the bay woodland, 11 were in the tree-fall-caused clearings in the center of the hill, and only 2 were encountered in oak woodland.

The four dbh transects uncovered no evidence of recruitment of *A. menziesii*—the only sapling located was a trunk-sprout from a fallen individual.

DISCUSSION

Bay woodland-forest. The bay woodland-forest of the lower hill and stream bank appears to represent the local climax community, or at least a preliminary version of it. Quantitatively, the most reliable evidence for this are the size-frequency data, which suggests that *Umbellularia californica* is the only major canopy member presently replacing itself in any numbers (Fig. 5). Although aerial photo comparisons could (ideally) provide more direct evidence for the scale and the rate of transition, the scope of this study did not permit the close scrutiny of aerial photos except for use as an aid in the determination of approximate contemporary vegetation type boundaries and areas.

A generalized vegetation map of the Garin Woods, compiled by

Rowlett in 1971, hints at the changes a quarter-century has wrought in the stands along Zeile Creek: her map shows at least a half-dozen *Alnus rhombifolia* and many *Acer macrophyllum* along the stream, and a large thicket of *Salix* spp. on the north bank just within the eastern boundary of the Ecology Field Station property. Field checking in 1994 found only one surviving *A. rhombifolia*, riparian stands of *A. macrophyllum* depleted by about 25%, and only two small specimens of *Salix lasiolepis* in place of Rowlett's thicket. Although *Alnus* spp. are intolerant of aggressive competition (Fowells 1965), fluvial downcutting may actually account for much of this change: trunks of both *A. rhombifolia* and *A. macrophyllum* (among other species) are found in the creek bed, and many other streamside trees are presently being undercut. The Zeile Creek stream bed is locally entrenched up to 2.5 m, a recent occurrence common to many East Bay streams, regardless of watershed urbanization (Rogers 1988); grazing in Garin/Dry Creek Pioneer Regional Park, and housing construction within the Zeile Creek watershed have almost certainly increased sediment load and peak flow amounts, increasing the local rate of streambank erosion and causing heavy siltation at Zeile Creek's mouth in Cemetery Pond (R. Benseler and R. Tullis, personal communication). Today, bay woodland covers almost the entire south bank of Zeile Creek within the study site. Some of these streamside stands are more than 90% *U. californica*, yet recruitment is still relatively high. The five point-quarter transects run closest to the creek showed a average of 39% *U. californica* in the middle story (compared with 3% *Q. agrifolia*).

The occurrence of several small, isolated specimens of *Quercus chryssolepis* may also provide some clues as to the successional history of the Garin Woods. These individuals occur under a closed canopy of *U. californica*, in association with *Heteromeles arbutifolia*, at an altitude of 150 m (50 m below the species' published range in the Jepson Manual). There are several defoliated boles nearby which resemble *Q. chryssolepis* as well. In the Carmel Valley (south of the Bay Area), Griffin (1974) noted a *Q. chryssolepis*-phase of mixed evergreen forest in shady canyons and on steep north-facing slopes. Canopy cover was dense, understory growth was light, and colonies of *U. californica* were scattered throughout the stand. With the dominant trees reversed, this description sounds much like the lower Garin Woods. Although these exotic *Q. chryssolepis* may be just that, one wonders if perhaps they (and *H. arbutifolia*—see below) are remnant flora from a more favorable climate, or grazing/fire regime?

The bay woodland vegetation type exhibits the lowest canopy and middle story densities in the Garin Woods, and the canopy is more dominated by a single species than in either of the other two broadleaf evergreen vegetation types (Table 2). As is common under *U. californica*-dominated canopies, the shrub layer is not well-devel-

oped (Cooper 1922; McBride 1974), and many of the shrub types are present in only one or two localities (*Salix* spp., *Garrya elliptica*, *Holodiscus discolor*, e.g.), where sufficient light reaches the forest floor and along the stream bank. The moist, low-light microclimate that results from this high, often closed canopy favors instead the growth of understory species such as *Polystichum munitum*, *Smilacina* spp., and *Disporum hookeri* (personal observation). Middle story complexity increases significantly with changes in aspect, and/or thinning of the canopy: the highest middle story densities in the bay woodland (>twice the average) are found along the western border, where the stand is more open to wind and afternoon sun and *Quercus agrifolia* comprises more of the canopy.

The index of dispersion ($\text{var./}\bar{x} = 1.803$) for the bay woodland vegetation type shows that canopy members are highly clumped in this stratum. This is hardly surprising, since *U. californica* commonly reproduces through sprouting and vegetative propagation, creating multi-stemmed clumps, especially where there are canopy openings to the side (Stein 1958). The middle story showed even more significant aggregation than the canopy ($\text{var./}\bar{x} = 1.999$). This would be expected in a community where canopy cover is high, and shafts of light reaching the ground are few and far between—precisely the situation in much of the lower Garin Woods.

The middle story in the bay woodland/forest is dominated by *Heteromeles arbutifolia* (toyon), which, unlike the other shrubs, is spaced relatively regularly throughout the vegetation type. This association with *U. californica* in a damp, low-light microclimate was not expected. *Heteromeles arbutifolia* is customarily associated with chaparral, or the drier, brushy edges of local forests and woodlands (Munz and Keck 1959; Ferris 1968), yet in the Garin Woods it was only infrequently encountered outside of bay woodland, and almost never seen in oak woodland (although field observations show it is common in the narrow oak woodland/grassland ecotone found along the western edge of the Garin Woods) (see Fig 3c). The elevated presence of toyon in the bay woodland could be explained in a number of ways. Field observations turned up very few *H. arbutifolia* seedlings or saplings, and many of the adult plants in the bay woodland are not healthy. Possibly, it is remnant of an earlier, more *Quercus*-dominated forest and has survived by default as middle story competition (especially from *T. diversilobum*) is essentially nonexistent, or because it has higher tolerance for the shade (and allelochemicals?) of the *U. californica*. It may also be that *H. arbutifolia* is more amenable to moist, shaded conditions than is commonly supposed: the author's observations suggest that *H. arbutifolia* is present in similar proportions in other, nearby stands of bay woodland; McBride (1971) found *H. arbutifolia* associated with moister, closed-canopy conditions, and in another study (1974) he

encountered no *H. arbutifolia* in any of the oak woodland he surveyed, yet it was a fairly common member of bay woodland stands.

Oak-bay woodland. To a certain extent, the small area classified as oak-bay woodland represents an agglomeration of more-or-less contiguous transects that do not obviously belong to either bay- or oak woodland. A strict definition of this zone is problematic, but some generalizations can be made about this vegetation type in the Garin Woods: 1) neither *Umbellularia californica* nor *Quercus agrifolia* clearly dominates the canopy; 2) canopy cover is locally sparse, or absent; 3) middle- and understory cover is dense; 4) species diversity, especially within the understory (personal observation), is high.

Field observation and data collected through point-centered quarter sampling suggest that the oak-bay woodland in the Garin Woods is more a transitional ecotone than a stable community. Canopy tree density was intermediate between the other two broadleaf evergreen vegetation types, but middle story density was >three times higher in the oak-bay woodland than in bay woodland, and 50% higher than in oak woodland (Table 2). The indices of dispersion for the oak-bay woodland provide further quantitative testimony to the transitional nature of this area. The canopy here is more random than that along the lower hill, yet more aggregated than that on the upper hill ($\text{var./x} = 1.52$). This is probably due to the more even proportions of *Q. agrifolia* and *U. californica* in this stratum. The measurement of dispersion for the middle story is extremely low ($\text{var./x} = 0.70$) (recall that 1 theoretically implies randomness, values >1 point to clumping, and <1 suggests a trend toward uniform distribution). Much of the canopy along the middle hill is open, allowing the growth of locally dense patches (scrub islands) of *Toxicodendron diversilobum*, *Holodiscus discolor*, *Ribes* spp., *Garrya elliptica*, and *Baccharis pilularis*. The cause for this is almost certainly the collapse of the local population of *Arbutus menziesii*.

Arbutus menziesii (madrone) comprised significantly more of the local tree canopy in the 1960's than it does today (R. Baalman, personal communication). Recent mass dyings have opened much of the Garin Woods' canopy, especially in the center of the hill. During point quarter and dbh sampling the author noted literally dozens of downed *A. menziesii* between transects Y2a and Y5b. Those remaining are often greatly defoliated and in the process of being overtopped by neighboring *U. californica*. Size-frequency measurements of both live and dead madrone produced a classic 'inverted bowl,' characteristic of species showing no recruitment (Fig. 5). It should be noted that this development is part of a wide regional trend. Madrone pathogens include trunk cankers, leaf galls and spots, and a spot anthracnose (Horst 1979) but the culprits most respon-

sible for this mortality have yet to be identified. Declining rainfall and higher temperatures are implicated in some circles (Benseler personal communication), but this seems unlikely, as *A. menziesii* grows best where summer soil moisture is low, and is even classified as drought resistant by the U.S.F.S. (Fowells 1965). Pelton (1962) found that seedling survival rates of madrone were extremely low, particularly in shaded conditions. In Pelton's study root-fungus and soil-dwelling invertebrates were implicated in about 60% of seedling mortality; drought *per se* accounted for 10% of seedling deaths. Madrone is often characteristic of secondary growth after logging or fire, especially from stump sprouts (Metcalf 1966); local conditions certainly do not presently favor this kind of growth. Field observations turned up only one *Arbutus* sapling in the entire Main Woods, sprouting from the cut stump of a tree that had fallen across a trail. At present *A. menziesii* comprises approximately 8.5% of the lower, bay woodland canopy, and about 7.4% of the higher oak-bay woodland: indications are that this proportion was greater in the past, and will be lower in the future.

The rapid disappearance of *Arbutus menziesii* from local forests and woodlands has important implications for the rate and direction of succession in parts of the Garin Woods. Islands of scrub presently fill many of the larger gaps created by *A. menziesii* treefall. Ground cover of *T. diversilobum*, *Rubus ursinus*, and *H. disolor* is locally very dense, and shrubby species like *Quercus palmeri* and *Baccharis pilularis* may reach heights of 4 m. Size-frequency measurements taken along the middle hill showed these open areas are fertile ground for recruitment of canopy species: 50% of all *Quercus agrifolia* seedlings sampled in Garin Woods occurred in these 'scrub islands,' as did >40% of all *Umbellularia californica* seedlings, and the only *Arbutus menziesii* seedling. Paradoxically, these openings in the canopy not only provide greater access to light and precipitation, but the well-developed shrub layer (in what has been called a nurse-plant relationship) affords better protection from predators and competing species, and helps to moderate climatic extremes (Callaway and D'Antonio 1991). This shrub layer is essentially absent in the bay woodland, and only moderately well-developed in the oak woodland. Taking into account that *U. californica* seedlings are still more than four times as common as *Q. agrifolia* seedlings in the oak-bay woodland, succession to a bay-dominated community appears to be inevitable, but indications are that transition to bay woodland has been significantly slowed by *A. menziesii* treefall.

Oak woodland. *Quercus agrifolia* is the dominant canopy species in this vegetation type; other oak members occur in the middle story of the scrubby woodland-grassland ecotone on the Garin Woods' southwestern edge. These include *Q. durata*, *Q. palmeri*, and a num-

ber of conspicuous hybrids, including a small (4–5 m), deciduous tree which occurs in a series of isolated copses ranged along the inner boundary of the ecotone. These are probably *Q. garryana* × *durata* (J. Tucker personal communication). The identification of *Q. durata* and *Q. palmeri* in the Garin Woods (confirmed by J. Tucker) represents a range extension for both species.

Indices of dispersion in the oak woodland are the most even in the Garin Woods (canopy = 1.31, middle story = 1.44). This can be accounted for by the stand habit of *Quercus agrifolia*, which is much less aggregated than that of *U. californica*, and the more open canopy of oak woodland, which allows for more middle- and under-story growth as well. *Toxicodendron diversilobum* and *Holodiscus discolor* blanket this stratum and are locally found in nearly impenetrable thickets; *T. diversilobum* is by far the dominant shrub in the oak woodland (Fig. 3e). *Heteromeles arbutifolia* and *Corylus cornuta* were only rarely encountered in point-quarter sampling: not a single example of either was sampled from the oak woodland portion of quadrat-row Z (although the author has seen a handful of each). The paucity of *H. arbutifolia* was unexpected: possibly it does not successfully compete with *T. diversilobum* in this environment.

Recruitment of *Quercus agrifolia* in the Garin Woods seems much too low to maintain the present adult population. Although the open canopy of conspecific adults and the relatively well-developed layer of nurse shrubs provide a healthy environment for seedling and sapling growth, recruitment of coast live oak in the oak woodland is practically nonexistent. On transects in this stratum, *Q. agrifolia* made up merely 5% of the middle story, and dbh sampling found only two saplings of ≤5 cm diameter (from 50 total samples). In contrast, 16% of the oak woodland middle story is constituted by *Umbellularia californica*, a figure with great portent for the future of this vegetation type.

Oak woodland/grassland ecotone. Floristically, the oak woodland-grassland ecotone is one of the more intriguing plant associations in the Garin Woods. The canopy in this zone is composed of stunted *Q. agrifolia* and *U. californica*, in more even proportions than elsewhere in the oak woodland, with the deciduous *Quercus* hybrid comprising the remaining 10%. Canopy height is noticeably less than within the oak woodland proper. Woody species found in this ecotonal strip which were not sampled or seen elsewhere in the oak woodland include: *Artemisia californica*, *Baccharis pilularis* (rare), *Quercus durata*, *Quercus palmeri*, *Rhamnus crocea*, and the various *Quercus* hybrids. Woody species which are significantly more common in the ecotone than in the oak woodland are *Garrya elliptica*, *Heteromeles arbutifolia*, *Mimulus aurantiacus*, and *Oemleria cerasiformis*. This ecotone apparently owes its existence to its west-

facing aspect and highly-exposed position, on the windward edge of the Garin Woods, atop a steep, 50 m high escarpment (thought to be the footwall of the West Chabot Thrust Fault by Dibblee (1980)). Wind-shearing has misshapen all of the exposed plants. An edaphic derivation for the ecotone has been postulated as well (R. Baalman, personal communication). Serpentine is known to occur along the northern continuation of the escarpment ridge, across Zeile Creek, and geologic maps suggest a continuation of this rock unit (the Coast Range Ophiolite sequence) into the western portions of the Garin Woods, but I (a geologist by training) found greatly altered basalt and rhyolite in the ecotone, but no obvious evidence of serpentine or allied minerals. More study is needed of this ecotonal community and the abiotic factors that influence it: the presence of *Quercus durata* suggests that serpentine may be one of those factors.

CONCLUSION

Evidence from all over California suggests that the present range of many oak species is shrinking (Griffin 1971; McBride 1974; Muick and Bartolome 1987; Callaway and D'Antonio 1991). Reasons for this decline may include changing climate, increased land development (Barrett 1979), changes in fire and grazing patterns (McBride 1974), and increased seedling predation by animals (Barrett 1979; Griffin 1979).

Cattle have not had access to the C.S.U.H. ecology field station for approximately 15 years, but the station's proximity to the Garin/Dry Creek Pioneer Regional Park means that a large and protected deer population may seasonally migrate in and out of the property. Browsing by livestock and deer may be the most significant impediment to oak regeneration in California (Barrett 1979). Grazing of coast live oak water shoots is locally heavy in the Garin Woods; the author noted heavily pruned *Q. agrifolia* even during the wet spring of 1994, when grass and forb availability was still high. Along the southern edge of the oak woodland, many coast live oak shrubs have been severely stunted by browsing as well. In addition to seedlings and water shoots, deer eat acorns as well (Barrett 1979, Griffin 1979); cattle also have enormous appetites for them (Duncan and Clawson 1979). Pocket gophers (*Thomomys bottae*), gray squirrels (*Sciurus grisius*), the dusky-footed wood rat (*Neotoma fuscipes*), scrub jays (*Aphelocoma coerulescens*) and the California quail (*Lophortyx californicus*), all of which are found on the study site, are other major consumers of oak acorns (Griffin 1979).

Fire is actively suppressed on the study site and in most of the increasingly populated Hayward Hills. Probably no major burn has occurred in at least the last 50 years, and possibly within this century. McBride (1974) found that the frequency of fire is one of the major

determinants of the relative proportion of oak and bay in the broadleaf evergreen forests. *Quercus agrifolia* is extremely fire resistant (Plumb 1979), but this adaptation is of little use in the present fire regime. The present lack of recurrent fire, and the heavy grazing of oak seedlings and acorns favors *Umbellularia californica* and its young which, unlike oak, germinate well under canopies of either species (Jackson 1973).

Evidence presented in this paper suggests that the oak woodland of the Garin Woods is a remnant of a formerly more extensive vegetation type. Barring a resumption of regular ground fire and a sudden cessation of browsing and acorn predation however, it would appear that much of the study site that is not already bay woodland may be in the not too distant future.

ACKNOWLEDGMENTS

I thank Dr. Susan Opp, Dr. Robert Baalman, and especially Dr. Rolf Benseler for their invaluable advice, assistance, and editorial comments, and my wife, Mary K. Safford, for her support and exhortation during the six month course of this study. Dr. John Tucker of the University of California, Davis, graciously identified all unusual oak species and hybrids, and Kathleen Culligan and Sylvia Mori provided editorial comments as reviewers of this paper. I also gratefully acknowledge the assistance of the East Bay Chapter of the California Native Plant Society, which helped to support this study with a Myrtle Wolf Scholarship, awarded in June, 1994.

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THE TAXONOMIC STATUS OF *LUPINUS CUSICKII* (FABACEAE)

S. L. BROICH AND L. A. MORRISON

Herbarium, Department of Botany and Plant Pathology,
Oregon State University, Corvallis, OR 97331-2902

ABSTRACT

We have reviewed the taxonomic status of *Lupinus cusickii* S. Watson, a rare Oregon lupine. Our research included study of herbarium collections, field populations, and a taximetric comparison of *L. cusickii* with related taxa. *Lupinus cusickii* is an element of the *Lupinus caespitosus-lepidus* complex and is best treated taxonomically as *L. lepidus* var. *cusickii*. Although the *L. caespitosus-lepidus* complex is widely distributed throughout western North America, var. *cusickii* is known from only five sites, all in western Baker County, Oregon. Further field survey work will be needed to determine the full extent of its distribution and its status as a rare and possibly endangered plant taxon. Keys and diagnoses to the varieties of *L. lepidus* occurring in eastern Oregon are presented.

Lupinus cusickii S. Watson has been considered a rare and possibly endangered Oregon plant species by Siddall et al. (1979) and by Meinke (1982). Efforts by the U.S. Bureau of Land Management and the Oregon Department of Agriculture to assess the status of *L. cusickii* in the field have been confounded by identification problems. The purpose of the research reported here was to review the taxonomic status of *L. cusickii*. Our investigation included studies of herbarium collections and extant populations in the field and a taximetric study of morphological variation within *L. cusickii* and closely related taxa.

TAXONOMIC HISTORY

Lupinus cusickii was described by Watson (1887) from specimens collected in July of 1886 by William Cusick along the Burnt River in what is now Baker County, Oregon. C. P. Smith (1924) reduced the epithet *cusickii* to varietal status under the name *Lupinus aridus* Douglas ex Lindley without comment. Later, he noted that var. *cusickii* "is an interesting connecting link between *L. aridus* and *L. caespitosus*, which also, perhaps, should be treated as a variety of *L. aridus*" (Smith 1927, p. 25). Smith considered *L. aridus* as part of a group he called the "caespitosi" in which he also included *L. caespitosus* Nutt., *L. lepidus* Douglas ex Lindley, and *L. lyallii* A. Gray. By 1946 Smith referred to the *caespitosi* as the "caespitosus-lepidus complex" consisting of "one to several species, according to the view-point of the botanist concerned" (Smith 1946, p. 547).

Detling (1951) concluded that the *L. caespitosus-lepidus* complex consisted of one species—*L. lepidus* Douglas ex Lindley—and described seven intergrading subspecies. He retained the epithet *cusickii* at the subspecific level. Phillips (1955), in his review of perennial *Lupinus* in western North America, reduced the epithet *cusickii* to synonymy under *L. lepidus*. Dunn (1956), however, maintained that the *L. caespitosus-lepidus* complex consisted of separate species. Following this view, Cox (1972a, b, 1973a, b, 1974a, b, c) described 10 species and 30 intra-specific taxa within the group. Both Dunn and Cox treated *cusickii* at the specific level; Cox (1973b) described three subspecies within *L. cusickii*. In floristic treatments, Smith (1944) and Peck (1961) listed *cusickii* as a variety of *L. aridus*. Hitchcock et al. (1961), Hitchcock and Cronquist (1973), Barneby (1989), and Sholars (1993) retained *cusickii* at the varietal level under *L. lepidus*. Historically, therefore, lupine populations referable to the epithet *cusickii* have been treated variously as a species and as a subspecies, variety, or synonym of *Lupinus lepidus*. For the remainder of this paper, we will discuss *cusickii* and other elements of the *caespitosus-lepidus* complex as varieties of *Lupinus lepidus* sensu lato.

MATERIALS AND METHODS

To get an overview of the *Lupinus caespitosus-lepidus* complex, we examined approximately 850 herbarium specimens from OSC, WILLU, ORE, WTU, WS, ID, IDS, MO, UMO, and NY and from herbaria maintained by the Bureau of Land Management at the Vale, Burns, Prineville, and Lakeview district offices in eastern Oregon.

During the summers of 1989 and 1993, the senior author visited 30 populations of caespitose lupine in Linn, Jefferson, Lake, Deschutes, Klamath, Crook, Harney, Grant, Baker, and Malheur counties in central and eastern Oregon to collect and make field observations. Three to fifteen plants were collected from each population visited; individual plants within populations were collected systematically so that the range of morphological variation present at the site would be represented in the study specimens.

Ninety-four individual plants collected from 13 populations studied in the field (Table 1) were incorporated into a taximetric study of morphological variation within the *L. caespitosus-lepidus* complex as it occurs in eastern Oregon. An additional 15 herbarium specimens of *L. lepidus* var. *utahensis* from Idaho and Wyoming and 20 herbarium specimens of *L. lepidus* var. *aridus* from the Columbia River Basin in eastern Washington and north-central Oregon were added to this study because collections of both *aridus* and *utahensis* have been made in eastern Oregon. We did not encounter either taxon in the field. All 129 specimens were measured for the

TABLE 1. LOCATIONS OF EASTERN OREGON POPULATIONS OF THE *L. LEPIDUS-CAESPITOSUS* COMPLEX INCLUDED IN THE TAXIMETRIC STUDY.

Population	Location				
	County	Township	Range	Section (s)	Elevation
A Hoodoo	Linn	T135	R8E	S26	1450 m
B Sisters	Jefferson	T135	R9E	S32	1015 m
C La Pine	Deschutes	T22S	R10E	S27	1300 m
D Ft. Rock	Lake	T26S	R13E	S28	1380 m
E Brothers-1	Deschutes	T22S	R18E	S6/7	1460 m
F Brothers-2	Deschutes	T21S	R18E	S19/30	1400 m
G Brothers-3	Deschutes	T21S	R19E	S11	1400 m
H Divine Ridge	Harney	T20S	R31E	S22	1600 m
I Baldy Mt.	Grant	T14S	R33E	S19	2130 m
J Oregon Canyon	Malheur	T40S	R40E	S11	2350 m
K Unity-1	Baker	T135	R37E	S1/2	1200 m
L Unity-2	Baker	T135	R37E	S10/11	1235 m
M Unity-3	Baker	T135	R37E	S3	1280 m
N var. <i>utahensis</i>	15 herbarium specimens from Idaho and Wyoming				
O var. <i>aridus</i>	20 herbarium specimens from Oregon and Washington				

20 morphological traits listed in Table 2. Means of three to five measurements were calculated for vegetative traits, inflorescence traits, and flower lengths. Data on additional floral characteristics are based upon one dissected flower from each specimen. Flower dissections were made using a technique modified from that described by Dunn (1954) for *Lupinus* flowers.

The final data-set was standardized. Relationships among the 15 populations listed in Table 1 were then analyzed by cluster analysis. Generalized distance (Mahalanobis' D^2) between populations was calculated using the programs POOLVCV and CVA of the NTSYS-pc program package (Rohlf 1987); cluster analysis was performed using the SAHN program of NTSYS-pc.

RESULTS

Herbarium studies. The *caespitosi* (Smith 1927) are readily recognizable from other species complexes of perennial lupines in western North America and appear to form a natural monophyletic unit (Detling 1951; Cox 1972a). In addition to the caespitose habit, the *caespitosi* are distinguished by the persistence of floral bracts during anthesis, by rather stout, short pedicels (usually <4 mm), by the lack of a spur on the calyx tube, and by a dorsally glabrous banner.

The *caespitosi* are widely distributed in western North America, occurring in Washington, Oregon, California, Idaho, Wyoming, Utah, and Colorado. Morphological variation within the complex is extensive. Taxa traditionally described within the *caespitosi* are relatively distinct and usually have different geographic distributions.

TABLE 2. MORPHOLOGICAL TRAITS INCLUDED IN TAXIMETRIC STUDIES OF THE *LUPINUS LEPIDUS-CAESPITOSUS* COMPLEX.

1) plant height to the top of the foliage (cm); 2) petiole length (cm); 3) number of leaflets; 4) average leaflet length (mm); 5) average leaflet width (mm); 6) complete inflorescence length (cm); 7) raceme length (cm); 8) number of flowers; 9) pedicel length (mm); 10) flower length (mm); 11) upper calyx lobe length (mm); 12) upper calyx lobe notch depth (mm); 13) lower calyx lobe length (mm); 14) banner petal length (mm); 15) banner petal width (mm); 16) wing petal length (mm); 17) wing petal width (mm); 18) keel petal width (mm); 19) number of ovules; 20) anther length of the longest anther present (mm).

However, herbarium collections contain numerous specimens that are morphologically intermediate between the entities traditionally described, particularly in areas where the geographic distributions of the various described taxa overlap.

Our study of herbarium specimens led us to conclude the following: (1) due to morphological intergradation, the *caespitosi* are best treated as a single polymorphic species consisting of nine (or more) varieties; (2) taken together, the recent taxonomic treatments of Barneby (1989) and Sholars (1993) present a complete treatment of all major elements within group; and (3) five of the nine varieties delimited by Barneby (1989)—var. *sellulus*, var. *utahensis*, var. *aridus*, var. *lobbii*, and var. *cusickii*—occur in eastern Oregon.

Field observations. We studied 30 populations of caespitose lupines in Linn, Jefferson, Deschutes, Klamath, Lake, Harney, Malheur, Grant, and Baker counties in central and eastern Oregon during the summers of 1989 and 1993. These populations ranged in elevation from 1200–2350 m and occurred in a variety of vegetation types including openings in subalpine forests, the *Pinus ponderosa* Zone, the *Juniperus occidentalis* Zone, and the shrub-steppe-*Artemisia tridentata* Zone (Franklin and Dyrness 1973). They were usually found in deep, sandy soils located in the lowest areas of the local landscape, often in vernally wet basins or along roadsides in places of water accumulation. Populations K, L, and M (Table 1) are unique because of their location on steep, exposed hillsides of eroding volcanic ash.

Phenology varied with elevation, location, and, seemingly, size of plant within a location. In populations visited in June and July of 1989 in eastern Deschutes County, larger plants appeared to flower in late June and early July whereas smaller plants did not commence flowering until late July. If larger plants are taken to be older, there may be some phenological isolation between older and younger plants growing in the same population.

Racemes of caespitose lupines flower acropetally and elongate as flowering progresses; peduncles also elongate during the flowering

process. In early stages of flowering, when only the proximal flowers in a raceme have opened, the raceme may appear to be capitate and be completely hidden by the foliage. In non-capitate types, both the raceme and the peduncle elongate; by the time distal flowers in the raceme have opened later in the season, the raceme emerges partially or completely beyond the leaves. Keys written for identification of different forms of caespitose lupine (including the one presented below) often use the trait of raceme exposure above the vegetative base to distinguish intraspecific taxa within the group. Assessment of raceme exposure is best made after distal flowers in the raceme have opened. When identifying plants collected earlier in the season, one should attempt to take subsequent raceme elongation into consideration.

Taximetric analyses. Figure 1 displays the dendrogram resulting from a Complete Linkage cluster analysis of the 13 field populations and the two collections of herbarium specimens included in the morphometric study (Table 1). The cophenetic correlation between the Generalized Distance matrix and the results shown in Figure 1 is 0.839. Similar results were obtained with other clustering strategies (UPGMA, Single Linkage, etc.) and with Canonical Variate Analysis (results not shown). We interpret these results to indicate that the 15 populations included in the study consist of five groups (Figure 1) corresponding to the five varieties of *L. lepidus* delimited by Barneby (1989).

DISCUSSION

The *Lupinus caespitosus-lepidus* complex consists of approximately nine relatively distinct but intergrading morphological entities. In our opinion, treatment of these morphological variants as separate species gives a false impression that they are more distinct than they appear to be in the herbarium record or in the field. We believe that the morphological extremes within the complex are best treated taxonomically as members of one polymorphic species *Lupinus lepidus* Douglas ex Lindley. The taxonomic treatments of Barneby (1989) and Sholars (1993) taken together offer a complete overview of the complex.

Our taximetric study indicated that at least five of the nine varieties of *Lupinus lepidus* occur in eastern Oregon. Populations of caespitose lupine from Jefferson, Deschutes, and Lake counties (populations B through G) included in the study are similar to one another and are referable to var. *sellulus*. Plants collected from Grant (population I) and Harney (population H) counties during this study clustered with specimens of var. *utahensis* from Idaho and Wyoming. Higher elevation, prostrate populations studied here (popu-

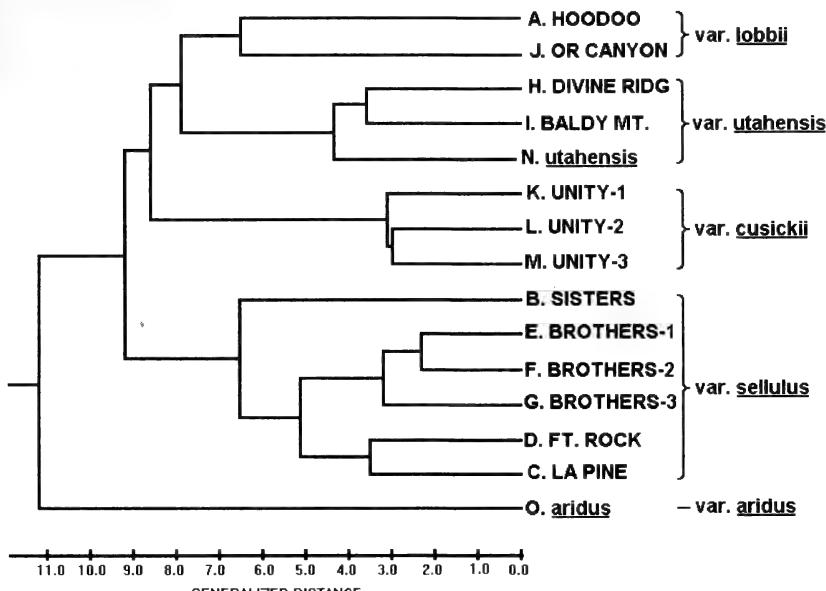


FIG. 1. Results of a Complete Linkage cluster analysis of the 15 populations of *L. lepidus* listed in Table 1.

lations A and J) are similar to one another and are best referred to var. *lobbii*. The collection of 20 herbarium specimens of var. *aridus* included in our taximetric studies proved to be quite distinct from other elements of the *caespitosus-lepidus* complex in eastern Oregon.

An isotype of *L. cusickii*, collected on a "sterile hillside of the upper Burnt Rio—above the forks" in July of 1886 by William Cusick (deposited in ORE) resembles plants collected from the three Unity sites (populations K, L, and M) included in our study. We conclude that the epithet *cusickii*, as originally conceived by Watson (1887), is referable to these Unity populations, interpreting the results of the taximetric study presented here to indicate that the Unity populations are distinctive. We believe that var. *cusickii* should be recognized within the *Lupinus caespitosus-lepidus* complex.

Cox (1973b) described two additional subspecies within his concept of *Lupinus cusickii*: subsp. *abortivus* (Greene) B. J. Cox and subsp. *brachypodus* (Piper) B. J. Cox. Type specimens of *L. abortivus* Greene and *L. brachypodus* Piper, deposited in ORE, appear to us to be referable to *L. lepidus* var. *aridus*.

A key to and diagnoses of the varieties of *L. lepidus* present in eastern Oregon is presented below. A more complete nomenclatural treatment for these taxa can be found in Barneby (1989).

**A KEY TO THE VARIETIES OF *LUPINUS LEPIDUS* IN
EASTERN OREGON**

1. Plants usually prostrate; peduncles 1.5–2.0 times longer than racemes; bases of caudices often woody; plants of alpine and subalpine meadows and forests. 1. var. *lobbii*
- 1'. Plants erect (although low growing); peduncles subequal to or shorter than racemes; bases of plants usually not woody; plants of lower elevation pine forests or sagebrush steppe 2
 2. Stem internodes extremely short (<1 cm), leaf bases telescoped into a caespitose clump; banners 2–3 mm wide 2. var. *utahensis*
 - 2'. At least some stem internodes elongated to 1–3 cm, leaf bases of upper leaves usually clearly separate; banners 4–6 mm wide 3
3. Mature racemes held above the basal tuft of leaves 3. var. *sellulus*
- 3'. Mature racemes partly or completely covered by foliage 4
 4. Plants generally >1 dm tall, upper stem nodes rarely branched; flower pedicels stout, 1–3 mm long 4. var. *aridus*
 - 4'. Plants generally <1 dm tall, upper stem nodes often branched; flower pedicels slender, 4–5 mm long 5. var. *cusickii*

1. *Lupinus lepidus* Douglas ex Lindley var. *lobbii* (A. Gray ex Greene)
C. L. Hitchcock (common synonyms: *L. lyallii* A. Gray; *L. lepidus* subsp. *lyallii* (A. Gray) Detling.)

Plants usually prostrate, sprawling, stems 4–10 cm long, sparingly branched at base, often arising from a woody caudex, upper stem internodes to 1 cm long, upper stem nodes usually unbranched; petioles 2–7 cm long, leaflets 5–21 mm long, 2–6 mm wide; peduncles 5–8 cm long, racemes 2–6 cm long, held above or away from the vegetative crown; pedicels 1–2 mm long at anthesis; banner blades 4–6 mm wide.

Habitat and distribution. montane and subalpine habitats along the Cascade-Sierra axis from British Columbia to central California extending eastward at higher elevations (>2000 m) in the Blue Mountains and into eastern Idaho; 1300–3000 m; in eastern Oregon: Clackamas, Crook, Douglas, Harney (Steen's Mt.), Hood River, Jackson, Klamath, Lake, Malheur (Trout Creek Mts.), and Wallowa counties.

Variety *lobbii* is readily identifiable on the basis of its prostrate habit, its long peduncles holding the capitate racemes beyond the foliage, and its distribution in higher elevation habitats. Variety *lobbii* appears to intergrade with var. *sellulus* along the eastern flank of the Cascade Mts. in Oregon (see the discussion of var. *sellulus*).

2. *Lupinus lepidus* Douglas ex Lindley var. *utahensis* (S. Watson)
C. L. Hitchcock (common synonyms: *Lupinus caespitosus* Nutt.
ex T. & G.; *L. lepidus* subsp. *caespitosus* Detling)

Plants more or less erect, 5–17 cm tall, stems sparingly branched

at base, upper stem internodes extremely short, leaves telescoped into a caespitose clump from which 1–3 inflorescences emerge; petioles 2–11 cm long, leaflets 10–30 mm long, 3–6 cm wide; peduncles to 1 cm long, racemes 2–8 cm long, usually barely emerging from the caespitose clump when distal flowers are mature; pedicels 1–2 mm long at anthesis; banner blades 2–3 mm wide.

Habitat and distribution. mountain meadows, gravel bars, streambeds, and lake shores, ascending up to stony crests near and above timberline (Barneby 1989) in eastern Oregon and extending east into Idaho, Wyoming, Utah and Colorado; 1200–2400 m; in Oregon: Union, Grant, Harney, and Umatilla counties.

Variety *utahensis* represents the most caespitose form of the *L. lepidus-caespitosus* complex and is distinctive for its lack of stem elongation that places the raceme within the vegetative clump.

3. *Lupinus lepidus* Douglas ex Lindley var. *sellulus* (Kellogg) Barneby

Plants erect, 3–14 cm tall, stems sparingly branched at base, upper stem internodes 1–3 cm long, upper stem nodes usually unbranched; petioles 3–9 cm long, leaflets 10–19 mm long, 3–7 mm wide; peduncles 5–8(–10) cm long, racemes 2–7 cm long, usually emerging well above the foliage when distal flowers are mature; pedicels 1–2 mm long at anthesis; banner blades 4–5 mm wide.

Habitat and distribution. vernally wet areas in ponderosa pine forests descending into juniper-sagebrush regions; east slopes of the Cascades from Deschutes County south into northern California; 1000–1900 m; in Oregon: Deschutes, Crook, Lake, Klamath, and Jackson counties.

Detling (1951) described a separate subspecies of *L. lepidus*—subsp. *medius* Detling—to include many of the lower elevation populations found on the eastern flanks of the Cascade Mts. in central Oregon. He believed *medius* to be an ancestral form within the complex. We find it difficult to recognize *medius* as a separate taxonomic entity. Central Oregon, from Sherman and Wasco Counties in the north to Lake, Klamath, and Jackson counties in the south, appears to be an area of general intergradation for the *lepidus-caespitosus* complex. Variety *sellulus* intergrades with var. *lobbii* along elevational gradients on the eastern flanks of the Cascades, and, seemingly, intergrades with var. *aridus* in Jefferson County and to the north. Varieties *sellulus* and *aridus* typically grow erect; var. *lobbii* is a prostrate form. Varieties *sellulus* and *aridus* differ mainly in plant height, peduncle length, and raceme length. This intergradation may be natural or it may be due to widespread disturbance of the vegetation in the area since European settlement. Whatever

the cause, it is well to recognize that assigning names to caespitose lupine populations in this area can be, at best, an inexact science.

4. *Lupinus lepidus* Douglas ex Lindley var. *aridus* (Douglas ex Lindley) Jepson

Plants erect, 1–2+ dm tall, stems sparingly branched at base, upper stem internodes 1–3 cm long, upper stem nodes usually unbranched; petioles 5–15 cm long, leaflets 20–35 mm long, 6–9 mm wide; peduncles 5–15 cm long, racemes 6–18 cm long, often emerging only partially from the vegetative clump when distal flowers are mature; pedicels 1–2 mm long at anthesis; banner blades 4–6 mm wide.

Habitat and distribution: lower elevations on bluffs and sandy or gravelly hillsides dominated by sagebrush or juniper woodland (Barneby 1989) in the Columbia River Basin and extending south and east; 100–1500 m; in Oregon: Baker, Crook, Deschutes, Galliam, Grant, Harney, Jefferson, Malheur, Morrow, Sherman, Umatilla, Wasco, and Wheeler counties.

Variety *aridus* intergrades with var. *sellulus* in Jefferson County, Oregon. In general, var. *aridus* tends to be taller and more robust than var. *sellulus* and, typically, the racemes of var. *aridus* emerge only partially from the foliage. The discussion of var. *sellulus* contains further details on intergradation in central Oregon.

5. *Lupinus lepidus* Douglas ex Lindley var. *cusickii* (S. Watson) C. L. Hitchcock

Plants erect, 2–11 cm tall, stems sparingly branched at base, upper stem internodes 1–3 cm long, each upper stem node often bearing a lateral branch terminating with an inflorescence; petioles 2–6 cm long, leaflets 7–19 mm long, 3–7 mm wide; peduncles 1–6 cm long, racemes 1–6 cm long, held at about the height of the vegetative crown; pedicels 4–5 mm long at anthesis; banner blades 4–6 mm wide.

Habitat and distribution. eroding hills of volcanic ash found along the Burnt River in Baker County, Oregon; 1200–1300 m; possibly also in Grant, Harney, Malheur, and Umatilla Counties.

Lupinus lepidus var. *cusickii* is unique in its cauline branching habit and its habitat. At the present time, populations of var. *cusickii* have been verified for five sites in eastern Baker County. We recommend that similar habitat in surrounding areas be surveyed to ascertain more completely the range of var. *cusickii* along the southeastern flanks of the Blue Mountains and to determine its status as a rare and possibly endangered plant taxon.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance given on this project by Robert Meinke, Kenton L. Chambers, Aaron Liston, Chris Mundt, Ron Halvorson, Kari Yanskey, Jim Kagan, and Jolene Broich. We also thank John Strother and two anonymous reviewers for their valuable contributions toward the improvement of this report. This research was funded by the Oregon Department of Agriculture and the Bureau of Land Management.

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ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY
16TH GRADUATE STUDENT MEETINGS

February 24, 1996

at Rancho Santa Ana Botanic Garden, Claremont

ATTENDANCE: Anyone may attend; registration is \$5.00. If you are presenting a paper, you must be a current or recent graduate student. Membership in the California Botanical Society is **not** required.

PRESENTATIONS: 10–12 minutes, plus 3–5 minutes for questions, on proposed, ongoing, or completed research in **any aspect of plant science**.

AWARDS: Cash awards will be given for best presentations in each research category. Students not giving talks, but with prior experience, are needed as awards judges.

BANQUET: The California Botanical Society Annual Banquet will be held at RSA following the graduate student meetings.

GUEST SPEAKER: Ken Berg, National Botanist for the Bureau of Land Management

TITLE: *Conservation of Native California Plants in the Changing Political Landscape*

HOUSING: A list of local hotels will be sent on receipt of registration. Limited space *may* be available with local students/faculty.

DEADLINE: **January 22, 1996** for registration materials and abstracts.

INFORMATION & FORMS: Forms will be available soon at botany/biology department offices. The \$5.00 graduate student meeting registration fee does not include the Annual Banquet. For further information, contact Lisa Schultheis, Graduate Student Representative, Integrative Biology, Valley Life Sciences Building, UC Berkeley, Berkeley, CA 94720, or (510) 643-7008, or lschult@violet.berkeley.edu.

ESTRUCTURA Y TENDENCIAS SUCESIONALES EN VEGETACION DE CLIMA TEMPLADO SEMI-SECO EN DURANGO, MEXICO

RENE CASAS S.

Escuela de Ciencias Forestales,
UJED, Durango, Dgo., Mexico

SOCORRO GONZALEZ E. Y JORGE A. TENA F.
CIIDIR y COFAA- IPN, Apdo. Postal 738,
Durango, Dgo., 34000 Mexico

RESUMEN

Tres asociaciones vegetales de clima templado semi-seco del estado de Durango, México, fueron estudiadas con el fin de conocer su estructura y tendencias sucesionales. En cada asociación se analizaron tres clases de tamaño de las especies leñosas, determinándose los valores de densidad, frecuencia y cobertura, así como los índices de diversidad y equitatividad. Mediante la comparación entre los valores de cada estrato se aprecian algunas tendencias de cambio en la vegetación. Aunque los patrones de regeneración y de mortalidad de las especies estudiadas no son aún conocidos, la presente regeneración de árboles parece insuficiente para reemplazar las poblaciones existentes en dos de las comunidades estudiadas. El bosque de *Pinus-Quercus* tiende a ser desplazado por matorral de manzanita (*Arctostaphylos pungens*), mientras que el de *Quercus eduardii*, más seco, está siendo substituido por matorral de *Dodonaea viscosa*. Lo anterior se confirma por la presencia de matorrales adyacentes con escasos relictos de bosque. El incremento de arbustivas está ligado a un avanzado estado de deterioro provocado por tala, sobrepastoreo e incendios.

ABSTRACT

This study was carried out in order to know the structure and to obtain a preliminary understanding of successional trends of three plant associations of temperate semidry climate in the state of Durango, Mexico. Three size classes in each association were sampled. Absolute and relative densities, aerial coverages and frequencies were determined, as well as diversity and equitability. Comparison of the values between each size class provided a projection of the current population trends. Natural patterns of regeneration and mortality of the studied species are still unknown, but the present regeneration and recruitment of trees in two of the communities seem to be insufficient to maintain the woodlands. The *Pinus-Quercus* woodland is being replaced by manzanita scrub (*Arctostaphylos pungens*), whereas the drier *Quercus eduardii* woodland is being replaced by *Dodonaea viscosa* scrub. Presence of adjacent scrubland with scarce tree relicts confirm the results. Increases of invader shrubs reflects an advanced deterioration due to logging, overgrazing and fires.

A excepción de los bosques de piñonero, es muy poco lo que se conoce en México sobre estructura, dinámica y regeneración de los bosques de clima templado seco y semi-seco. En la Sierra Madre Occidental estos bosques se localizan entre el bosque templado-

húmedo y los pastizales o matorrales del Altiplano, en altitudes que fluctúan entre los 1900 y 2500 m en las laderas a sotavento, o tan bajas como 1500 m en el declive occidental, entre el bosque templado y el tropical caducifolio. En Durango las comunidades más representativas de estos ecosistemas son los bosques de *Quercus grisea* puro o asociado con *Q. arizonica*, *Q. hartwegii*, *Q. chihuahuensis* o *Q. laeta*; los bosques de *Pinus cembroides*, así como los de *Quercus emoryi* o de *Q. eduardii*, puros o asociados con *Q. coccobifolia*, *Q. hartwegii*, *Q. grisea*, *Arbutus arizonica*, *Pinus cembroides* o *P. chihuahuana* (González, 1992). Las partes más secas presentan elementos de matorral xerófilo, especialmente *Acacia schaffneri*, *Mimosa biuncifera* y *Opuntia* spp. Gordon (1968) y May-silles (1959) llevaron a cabo estudios en bosques templado-húmedos en Durango y González et al. (1993) estudiaron bosques tanto húmedos como semi-secos de la Reserva La Michilía. En este trabajo se describe la estructura de tres comunidades vegetales de clima templado semi-seco.

Extensas áreas de bosque en la Sierra Madre Occidental se encuentran perturbadas y la vegetación secundaria resultante ha sido escasamente documentada. Las comunidades estudiadas en este trabajo han sido explotadas durante mas de cuatro siglos como fuente de leña y carbón para uso doméstico y de la industria del hierro en la ciudad de Durango y anteriormente por ser asentamiento de culturas precolombinas (Hendricks 1958). Los frecuentes incendios, el sobrepastoreo y la extracción de leña, aunados a condiciones climáticas poco favorables han provocado innumerables cambios en la vegetación. El patrón temporal de cambio en la vegetación puede apreciarse mediante la descripción de incremento y decremento de poblaciones de especies particulares (Pickett et al. 1987) y su relación con algunos factores de disturbio (Pickett y McDonnell 1989). Las interacciones con herbívoros y patógenos pueden ser de importancia crítica en el curso de la sucesión (Connell y Slatyer 1977) y, aunados a factores "modificantes" (Pickett et al. 1987) como bajo vigor de los árboles, ataque de plagas y requerimientos de germinación no alcanzados, inciden en una escasa regeneración de pinos y encinos. Aunque es aventurado conjeturar sobre tendencias sucesionales en asociaciones no estables (Parker y Peet 1984), la información aportada en este trabajo puede fundamentar investigaciones futuras y ser útil para reorientar los programas de manejo del área.

AREA DE ESTUDIO Y METODOS

El estudio se realizó en tres sitios aledaños a la ciudad de Durango, en el estado de Durango, México, entre los 23°50' y 23°55'N y 104°40' y 104°46'W, en los ejidos La Ferrería, El Nayar y la comunidad de Santiago Bayacora, entre los 2000 y 2400 m s.n.m.

Las estaciones climatológicas más cercanas son El Pueblito y Santiago Bayacora, a 2000 y 1990 m s.n.m., con períodos de registro de 29 y 27 años, respectivamente. El Pueblito reporta una precipitación media anual de 538.7 mm y temperatura media anual de 17.6°C, mientras que en Santiago Bayacora la precipitación es de 580.5 mm y la temperatura media es de 19°C. El periodo de sequía está comprendido entre enero y mayo. De acuerdo a la clasificación de Köppen, adaptada para México por E. García (1964), el clima es de tipo BS₁kwe: seco estepario y templado semi-seco con régimen de lluvias de verano y extremoso.

La determinación de las principales asociaciones vegetales del área se llevó a cabo mediante revisión de fotografías aéreas a escala 1:20,000, así como recorridos de reconocimiento y verificación. Tres asociaciones fueron seleccionadas con base en su extensión y representatividad de la vegetación en la región: bosque de *Pinus-Quercus*, bosque de *Quercus* y bosque de *Quercus-Juniperus-Pinus*. Los muestreos se llevaron a cabo entre Noviembre de 1992 y Mayo de 1993. En cada una de las asociaciones fueron determinados los valores de densidad, cobertura, frecuencia e índice de valor de importancia de las especies leñosas, utilizando el Método de Cuadrantes Centrados en un Punto (Cottam y Curtis, 1961, descrito por Mueller-Dombois y Ellenberg, 1974). Para cada asociación se muestrearon 60 estaciones distribuidas en tres clases de tamaño: a) árboles (>2 m altura en *Pinus*; >1.4 m altura en *Quercus*, *Juniperus* y *Arbutus*); b) arbustos y/o juveniles de especies arbóreas (<2 m y >31 cm en *Pinus*; <1.4 m y >16 cm en *Quercus*, *Juniperus* y *Arbutus*); c) plántulas (<31 cm altura en *Pinus*, <16 cm en *Quercus*, *Juniperus* y *Arbutus*). Las plántulas de especies arbustivas no fueron muestreadas ya que, debido a su abundancia, su registro impide inventariar la regeneración de especies arbóreas, objetivo principal del presente estudio. Las clases de tamaño fueron definidas con base en registros sobre las alturas al alcanzar la edad adulta de especies arbóreas en Durango (González et al., no publicado), y se aplican únicamente para las especies y las condiciones registradas en este trabajo, ya que bajo otras condiciones (ej. en Mikan et al., 1994) individuos hasta de 1.5 m son considerados como plántulas. Para cada asociación el primer sitio de muestreo se estableció al azar, mientras que los siguientes fueron ubicados a 20 metros de distancia del último punto medido, siguiendo una línea diagonal a la dirección de las laderas, con el fin de incluir en lo posible las diferencias altitudinales en lomeríos y laderas de corta longitud. La variación estadística entre sitios fue determinada mediante análisis de varianza (ANOVA) de una sola vía, comparando las medias mediante la prueba t de Student. La nomenclatura es de acuerdo a González et al. (1991). La comparación entre los parámetros registrados para cada clase de tamaño permitió apreciar la estructura de la vegetación y predecir sus ten-

dencias de cambio a corto plazo. Este método ha sido aplicado como indicador de las tendencias sucesionales en diferentes asociaciones (ej. Peet y Loucks 1977; Sosa y Puig 1987; Quintana y González 1993; González et al. 1993) y algunas de sus limitaciones son discutidas por Austin (1977), Peet y Christensen (1980) y González et al. (1993). Su elección se basó en la carencia de comunidades equivalentes no perturbadas para comparación, en la escasa factibilidad de permanencia de puntos de muestreo periódicos para estudios a largo plazo y en la consideración acerca de las limitaciones de otros métodos (Loeb 1990).

Aunque no existen registros formales sobre la historia de manejo del área, con base en registros anecdotales, registros históricos generales y observaciones directas, factores de influencia humana fueron considerados en la interpretación de los datos.

Indices de riqueza de especies, de diversidad y de equitatividad fueron usados para complementar la información. La riqueza se estimó con el índice de Margaleff: $R = S - 1/\ln(n)$ y la diversidad mediante la fórmula de Shannon-Wiener: $H' = -\sum(n_i/N) \ln (n_i/N)$. Para calcular la equitatividad se usó la fórmula: $E_1 = H'/\ln(S)$, donde S representa el número total de especies en la muestra, n el número total de individuos registrados, n_i el valor de densidad absoluta de cada especie y N la densidad absoluta total (Ludwig y Reynolds, 1988).

RESULTADOS

Estructura y regeneración.

1. *Bosque de Pinus-Quercus.* *Pinus chihuahuana* y *Quercus eduardii* son las especies dominantes en un bosque muy abierto, con escasos elementos de *Quercus grisea*, *Q. chihuahuensis* y *Q. arizonica* (Figura 1). El estrato de juveniles y arbustivas está dominado por manzanita (*Arctostaphylos pungens*), cuyo valor de importancia supera en gran medida el valor conjunto de todas las demás especies y cuya densidad absoluta representa el 67.55% del total en ese estrato, en el que las arbustivas predominan sobre las juveniles de árboles. También el inventario de plántulas indica baja regeneración de especies arbóreas y las expectativas de permanencia de *Q. arizonica*, *Q. grisea* y *Q. chihuahuensis* en el área son muy limitadas. *Q. chihuahuensis* presenta 10 árboles/ha pero únicamente 1 plántula y ningún individuo juvenil en la misma superficie, en contraste con lo encontrado por González et al. (1993) en que la densidad de esta especie es 3 veces superior en el estrato inferior en un bosque de *Q. grisea* en un área protegida.

Como resultado del disturbio, muchos individuos de *P. chihuahuana* en el área presentan severa incidencia de muérdago (*Arceut-*

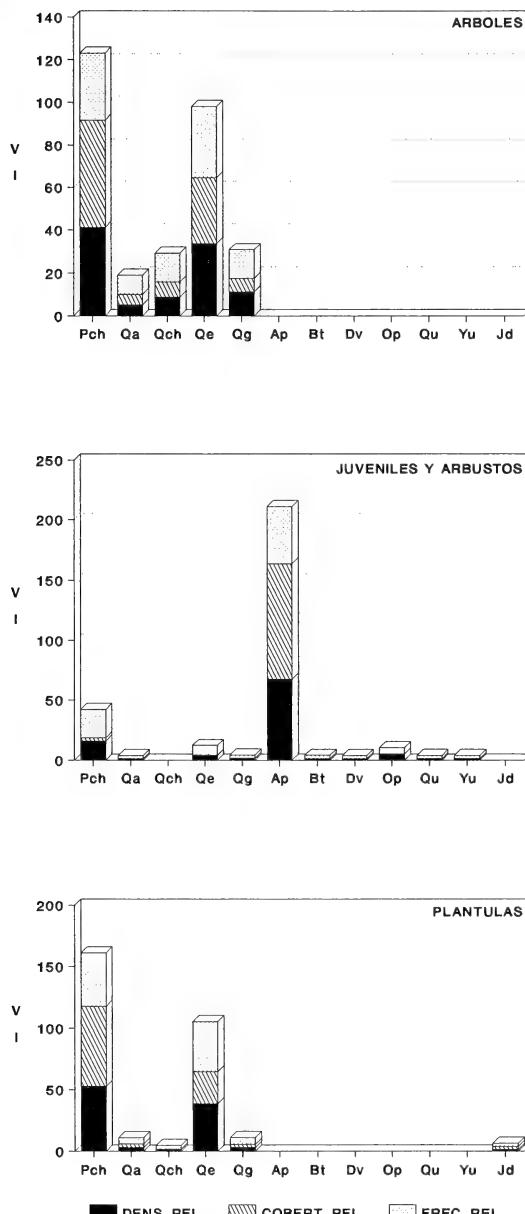


FIG. 1. Valores de importancia en tres estratos de bosque de *Pinus-Quercus*: Pch = *Pinus chihuahuana*; Qa = *Quercus arizonica*; Qch = *Q. chihuahuensis*; Qe = *Q. eduardii*; Qg = *Q. grisea*; Ap = *Arctostaphylos pungens*; Bt = *Bouvardia ternifolia*; Dv = *Dodonaea viscosa*; Op = *Opuntia* spp.; Qu = *Q. undata*; Yu = *Yucca* sp.; Jd = *Juniperus deppeana*.

hobium sp.) y del hongo *Cronartium conigenum*, mientras que las especies de *Quercus* son afectadas por larvas de insectos que reducen la viabilidad de la semilla.

2. *Bosque de Quercus*. El encino colorado (*Quercus eduardii*) es dominante en una comunidad muy abierta con escasos *Q. chihuahuensis*, *Q. cf. conzatii*, *Q. grisea* y dos híbridos (Fig. 2). *Q. eduardii* presenta una densidad de 42 árboles/ha, lo que representa casi un 80% del total. En el estrato medio el arbusto *Dodonaea viscosa* ("matagusano") es dominante florística y fisonómicamente (Fig. 3). *A. pungens* destaca en sitios sometidos a incendios controlados para favorecer el crecimiento de gramíneas forrajeras, mientras que xerófitas como *Agave*, *Mimosa*, *Dasyllirion* y *Yucca* se desarrollan en áreas con poco suelo.

La única especie arbórea que presenta regeneración es *Q. eduardii*, aunque también en este sitio la viabilidad de su semilla se ve afectada debido a insectos. La mayor parte de los encinos adultos presentan bifurcaciones desde la base o son retoños de tocones, indicando una intensa explotación en épocas pasadas. La presencia de *Q. cf. conzatii* en el área es de particular interés por constituir los primeros registros de esta especie para el norte de México. Bacon y Spellenberg (en preparación) presentarán evidencia al respecto.

3. *Bosque de Quercus-Juniperus-Pinus*. De 10 especies arbóreas y 2 arbustivas registradas (Fig. 4) los dominantes fisonómicos son el pino chino (*P. chihuahuana*) y el pino real (*P. engelmannii*), aunque su densidad es baja. El alto valor encontrado para *J. deppeana* está dado en función de su cobertura y su frecuencia, pero *Q. eduardii* presenta mayor densidad. La escasa cobertura en las especies de encino se debe a que en su mayoría, éstos son retoños a partir de tocones. En el estrato de juveniles y arbustivas predominan los arbustos *A. pungens* y *Quercus microphylla*.

Juniperus deppeana, *Q. eduardii* y *Q. microphylla* presentan una alta regeneración. Al igual que otras heliófilas, *Juniperus* se ha visto favorecida por los aclareos y tala de árboles.

Diversidad. En el bosque de *Pinus-Quercus* el estrato arbóreo presenta menor riqueza florística pero mayor diversidad y equitatividad que los estratos inferiores. Por el contrario, en el bosque de *Quercus-Juniperus-Pinus* la riqueza florística es mayor en el estrato arbóreo. La mayor riqueza y diversidad entre los árboles en esta comunidad indica una relativa homogeneidad en la abundancia de sus componentes, pero su equitatividad es ligeramente inferior a la del bosque de *Pinus-Quercus*, lo cual implica una distribución irregular

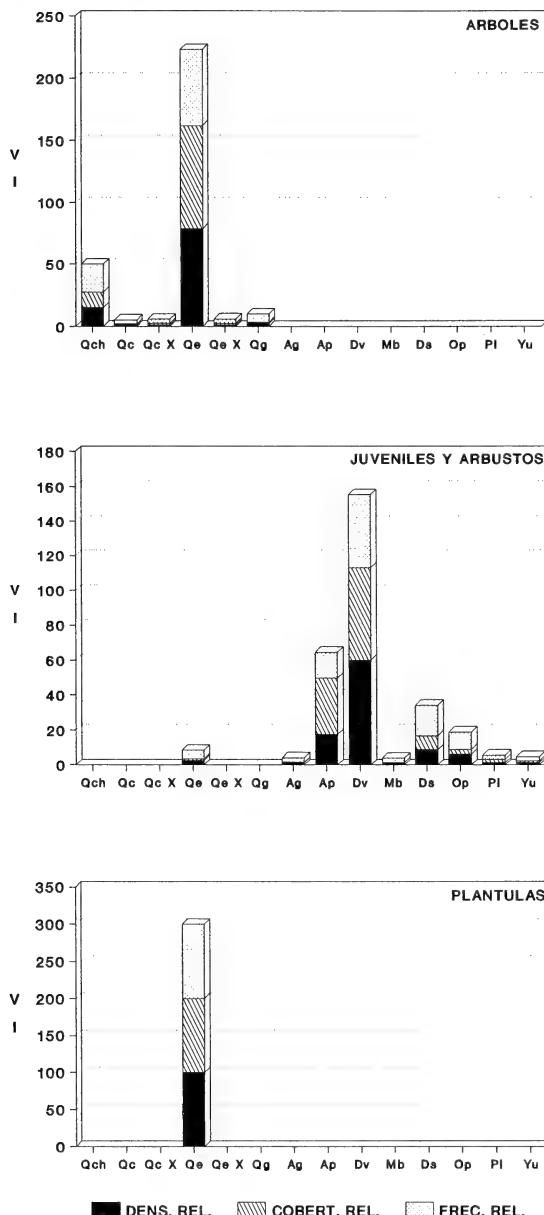


FIG. 2. Valores de importancia en tres estratos de bosque de *Quercus* spp.: Qch = *Quercus chihuahuensis*; Qc = *Q. cf. conzattii*; QcX = *Q. cf. conzattii* × *Q. eduardii*; Qe = *Quercus eduardii*; QeX = *Q. eduardii* × *Q. cf. conzattii*; Qg = *Q. grisea*; Ag = *Agave* sp.; Ap = *A. pungens*; Dv = *D. viscosa*; Mb = *Mimosa biuncifera*; Ds = *Dasylirion* sp.; Op = *Opuntia* sp.; Pl = *Prosopis laevigata*; Yu = *Yucca* sp.

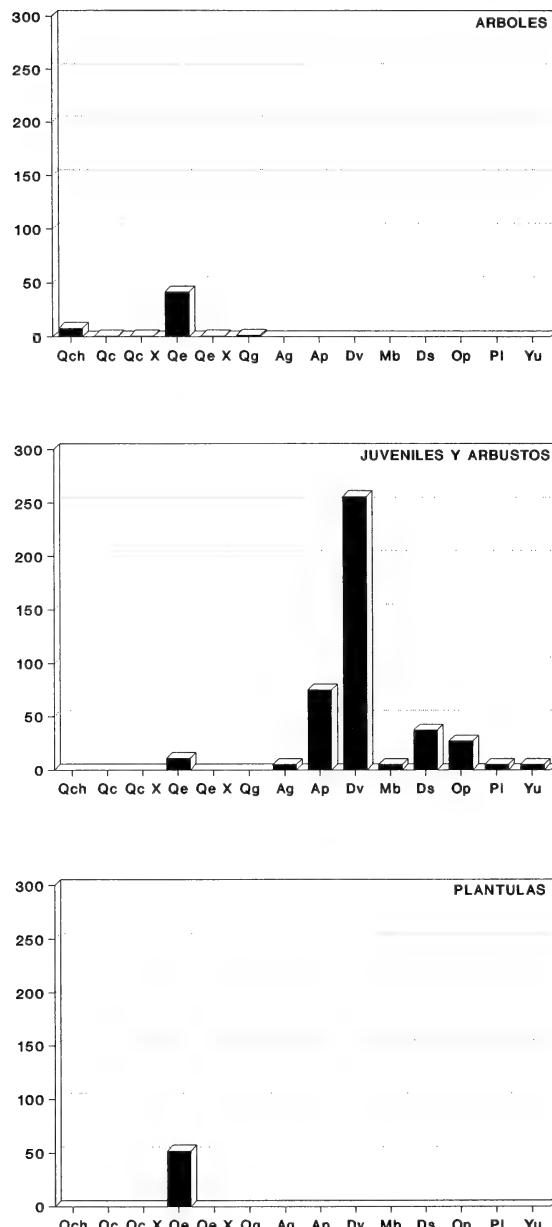


FIG. 3. Individuos/Ha en tres estratos de bosque de *Quercus* spp. Para simbología ver Figura 2.

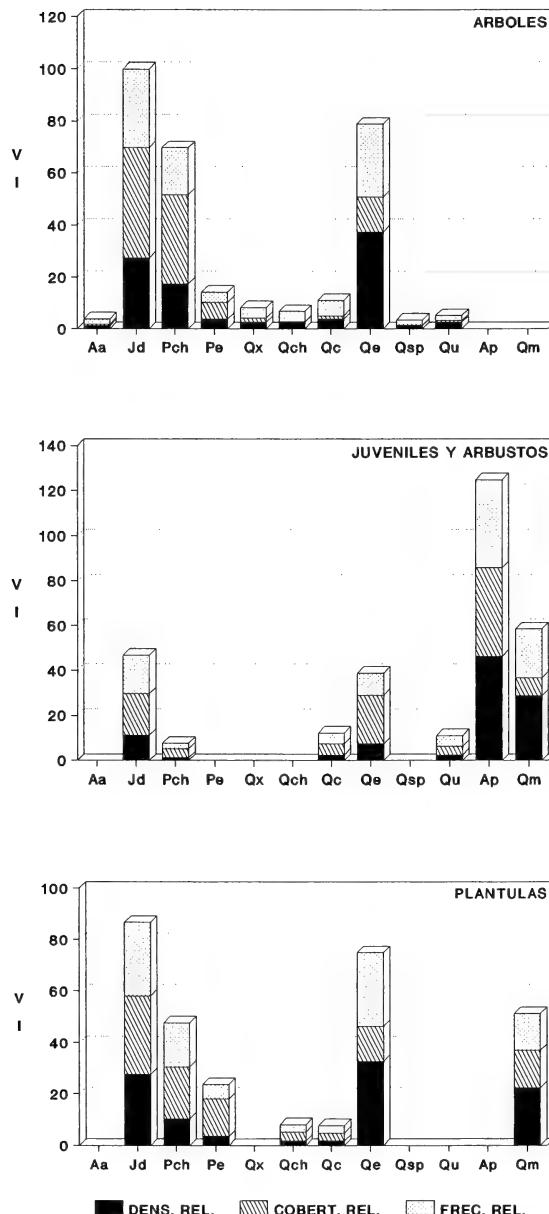


FIG. 4. Valores de importancia en tres estratos de bosque de *Quercus-Juniperus-Pinus*: Aa = *Arbutus arizonica*; Jd = *Juniperus deppeana*; Pch = *Pinus chihuahuana*; Pe = *P. engelmannii*; Qx = *Quercus chihuahuensis* X; Qch = *Q. chihuahuensis*; Qc = *Q. coccologifolia*; Qe = *Q. eduardii*; Qsp. = *Quercus laeta*; Qu = *Q. undata*; Ap = *A. pungens*; Qm = *Q. microphylla*.

CUADRO 1. RIQUEZA E INDICES DE DIVERSIDAD Y EQUITATIVIDAD EN BOSQUES DE CLIMA TEMPLADO SECO DEL SUR DE DURANGO.

	Riqueza (Margaleff)	Diversidad (Shannon- Wiener)	Equitatividad (Pielou)
Bosque de Pinus-Quercus			
Arboles	0.91	1.34	0.83
Juveniles y arbustos	2.50	1.15	0.50
Plántulas	1.14	1.00	0.56
Bosque de Quercus			
Arboles	1.14	0.77	0.43
Juveniles y arbustos	1.83	1.30	0.59
Plántulas	0.00	0.00	1.7E + 38
B. de Quercus-Juniperus-Pinus			
Arboles	2.05	1.63	0.71
Juveniles y arbustos	1.37	1.39	0.72
Plántulas	1.37	1.55	0.79

entre sus proporciones (Cuadro 1). La comunidad de *Quercus* presenta la mas baja diversidad y equitatividad en el estrato superior, debido a la manifiesta prevalencia de *Q. eduardii*.

Las medidas de diversidad han sido usadas como indicadoras de disturbio ambiental. En términos generales, en ambientes perturbados ocurre una desviación en el patrón de abundancia de especies y un decremento en la riqueza específica (Magurran 1988), aunque existe amplia discrepancia sobre los patrones que ocurren: Peet (1978) y Peet & Christensen (1980) sugieren que durante la sucesión ocurre un incremento inicial en la diversidad, pero que ésta se hace mínima durante las etapas de aclareo natural del bosque. A niveles intermedios de disturbio se genera la máxima diversidad y heterogeneidad espacial en habitats caracterizados por colonización y competencia, pero esto varía dependiendo de los niveles de resolución considerados (Kolasa y Rollo 1991; Tilman y Pacala 1993). En el modelo presentado por Armesto et al. (1991) para sucesión secundaria, periodos de alta y baja heterogeneidad se alternan y los períodos de alta heterogeneidad representan invasión y establecimiento de especies. Comparadas con las diversidades reportadas por González et al. para otros bosques de Durango, las comunidades estudiadas en este trabajo presentan una baja diversidad ($H' = 0.77-1.63$) y una estructura irregular, concordante con las evidencias de disturbio registradas. En los bosques de *Pinus-Quercus* y de *Quercus-Juniperus-Pinus*, la baja diversidad en el estrato medio en relación con el estrato superior se debe a la prevalencia de 1 o 2 especies sucesionales, las cuales se comportarían como declinantes en bosques relativamente no perturbados (Rhoades, 1992). En la comu-

nidad de *Quercus* el estrato superior presenta una diversidad aún mas baja, determinada tanto por la menor riqueza específica como por la dominancia de *Q. eduardii*. Si la hipótesis de diversidad pico en niveles de disturbio intermedio (con las mas bajas diversidades en ambientes no perturbados o muy altamente perturbados) es correcta, esta comunidad podría ser considerada como la más altamente perturbada; sin embargo, no es posible establecer conclusiones al respecto debido a la carencia de evidencias adicionales.

DISCUSIÓN Y CONCLUSIONES

Los tres sitios estudiados presentan asociaciones secundarias mantenidas por disturbio antropogénico. Las especies de *Pinus* y *Juniperus* en el área son heliófilas y por lo tanto favorecidas por los aclareos y algunas especies de *Quercus* son tolerantes al disturbio; sin embargo, a pesar de que el bosque es abierto, la regeneración de esas arbóreas es baja y en dos de los sitios estudiados el bosque aparentemente está siendo reemplazado por matorrales. La tolerancia a la luz o a la sombra no es en este caso determinante para el establecimiento de nuevos individuos, pero la escasa cobertura del dosel superior si afecta a la germinación y el establecimiento de plántulas al no existir protección contra la erosión, especialmente a principio de la época de lluvias, cuando no existe cobertura herbácea.

La baja densidad de árboles en el bosque de *Pinus-Quercus* se debe en parte a las condiciones ambientales poco favorables (escasa humedad y suelo somero), en parte a la tala clandestina (aún prevalente en el área) y en parte al impacto del ganado, ya que las plántulas de pino y encino son particularmente sensibles al efecto del pisoteo y pastoreo. Aunque el pastoreo moderado puede tener efectos positivos al eliminar herbáceas que estorban para la germinación de especies arbóreas y al eliminar acumulación de combustibles, este no es el caso en la comunidad estudiada.

La comunidad de *Quercus-Juniperus-Pinus* está sometida a frecuentes incendios provocados con el fin de inducir el crecimiento de gramíneas para pastoreo. *J. deppeana*, *Q. eduardii* y en menor grado *P. chihuahuana* y *P. engelmannii* mantienen regeneración por semilla, pero los arbustos *A. pungens* y *Q. microphylla* predominan ampliamente. *Pinus* y *Juniperus* han sido substituidos por chaparral en California debido a fuegos severos (Hanes 1971). Durante este estudio no fueron determinados índices de mortalidad, pero observación directa permite apreciar que la mortalidad en la comunidad de *Quercus-Juniperus-Pinus* es por lo menos mas baja que en las otras dos comunidades analizadas. Si se considera que valores tan bajos como 5 árboles/ha por década pueden ser suficientes para el mantenimiento de bosques en California cuando la mortalidad es baja (Mensing 1992), la regeneración observada en esta comunidad

puede ser suficiente para la persistencia del bosque, con un incremento en la densidad de arbustos en el sotobosque. Tanto *A. pungens* como *Q. microphylla* son indicadores de incendios recurrentes y se pueden presentar con *J. deppeana* en asociaciones secundarias derivadas de bosques de pinos (Rzedowski 1978), lo que podría ser el caso en el área estudiada.

En el encinar de *Q. eduardii* los valores de regeneración son bajos y la estructura en los estratos de juveniles y de plántulas difiere de manera conspicua de la del estrato superior, en contraste con lo encontrado para un bosque dominado por la misma especie en un área actualmente protegida (González et al. 1993). La comparación de estructuras entre estratos, la dominancia de *Dodonaea viscosa* y la presencia de matorrales casi puros de *Dodonaea* en áreas adyacentes sometidas a perturbación mas intensa, indican que el encinar está siendo desplazado por esa especie introducida de afinidad tropical.

Entre las especies arbóreas del área, *Q. eduardii* es la que presenta mayor tolerancia al disturbio gracias a su capacidad de regeneración a partir de tocones (después de cortes) y de la parte subterránea del tallo (después de fuego), a pesar de lo cual presenta indicios de declinación. Sus plántulas compiten por nutrientes con las de *Dodonaea* y *Arctostaphylos*, y enfrentan factores ambientales adversos que estos arbustos superan gracias a una mayor resistencia al fuego, mejor desempeño en áreas de disturbio y en suelos someros, y al hecho de que su follaje no es palatable al ganado, en contraste con lo encontrado por Reich et al. (1990) para áreas menos secas donde los encinos juegan el papel desempeñado aquí por el matagusano y la manzanita.

La regeneración de *Quercus* a partir de tocones se ha citado como factor importante en el encauzamiento de las fases de sucesión secundaria (Rzedowski 1978; Mensing 1992; Crow et al. 1994). Aunque algunos encinares desaparecen por falta de resistencia a incendios y falta de regeneración (Rzedowski 1978; Abrams and Nowacki 1992), por lo menos en bosques húmedos el reemplazamiento de encinos por otras especies se debe a la eliminación o supresión de fuegos (Crow 1988; Abrams y Downs 1990; Abrams 1992). Para bosques secos, pobres en nutrientes, donde no hay competencia de especies tolerantes a la sombra, se considera que *Quercus* puede mantener poblaciones estables no dependientes del fuego (Abrams 1992; Mikan et al. 1994); sin embargo, en los bosques secos aquí estudiados los incendios parecen ser un fenómeno natural al que la vegetación local estuvo adaptada hasta hace pocas décadas, antes de que la ocasional pérdida de control en la intensidad de incendios provocados condujera a una declinación en las poblaciones de especies arbóreas.

Es probable que la composición de las comunidades estudiadas

haya estado gradualmente modificándose durante por lo menos 400 años debido a la influencia humana, y anteriormente siguiendo ciclos naturales, pero las especies dominantes han sido arbóreas (Hendricks 1958). Aunque los patrones de regeneración de las especies estudiadas no son aún conocidos, la regeneración actual parece estar ligada a un incremento en las presiones ambientales. La tendencia de substitución por arbustos implica un cambio drástico en la dinámica de la vegetación del área, ya que los matorrales de *Arctostaphylos*, una vez establecidos, no permiten el restablecimiento del bosque a corto plazo. *A. pungens* es una especie con amplia tolerancia ecológica que juega diferentes papeles en el desarrollo de las comunidades: se presenta ya sea como componente del sotobosque en bosques no perturbados, o como dominante en densos matorrales similares en varios aspectos al chaparral californiano. Estos matorrales pueden ser de origen natural y aparentemente estables, especialmente en sitios sometidos a intensos vientos desecantes, o ser resultado de disturbio, en cuyo caso la manzanita obstaculiza la regeneración de árboles debido a su densidad, relación con fuego y acidificación del suelo. Es probable que la dominancia de *A. pungens* represente en ciertos casos parte de un ciclo de cambios gradual pero continuo al que se encuentra sometida la vegetación debido a la fluctuación de recursos y a los regímenes de disturbio naturales. Sin embargo, debido a la condición secundaria de las áreas aquí estudiadas no es posible predecir el impacto que la dominancia de este arbusto puede causar.

AGRADECIMIENTOS

Damos las gracias a Efrén Unzueta A. y Pablo Ibarra H. por su apoyo en el trabajo de campo. A Martha González E. y Lorena López por la ayuda en diferentes aspectos del trabajo. Al Dr. Richard Spellenberg por la identificación de *Quercus conzatii*, al M.C. J.A. Prieto, Ing. S. Bendímez, Ing. F. Sánchez y a Nir Gil-ad por sus comentarios sobre un texto preliminar y a dos revisores anónimos cuyas sugerencias permitieron mejorar substancialmente el manuscrito.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

RANUNCULUS HYDROCHAROIDES A. Gray (RANUNCULACEAE)—Inyo Co., Owens Valley, pasture irrigation ditches on Los Angeles Department of Water and Power land near Bishop, 1271 m, 27 Aug 1994, D. W. Pritchett 144 verified by A. Whittemore (Missouri Botanical Garden); Mono Co., Sierra Nevada, Inyo National Forest, uncommon in streambed of Mill Creek, ca. 2.7 km downstream from Lundy Lake, 2268 m, 5 Jul 1993 M. O. Bagley 4447; same location, 23 Jun 1994, M. O. Bagley 4531; same location, 14 Jul 1994, M. O. Bagley 4639; these three collections verified by D. H. Wilken (Santa Barbara Botanic Garden).

Previous knowledge. This species was known from California only in the Owens Valley, Inyo Co. (Munz and Keck, *A California Flora and Supplement*, 1968, who noted that it had been collected by Kellogg in 1874). The populations nearest to the Owens Valley were reported to be in northern Baja California (>450 km distant) and in the San Francisco Peaks area of Arizona (>550 km distant); it was also reported in the mountains of northern and eastern Arizona, western New Mexico, and in Mexico from Baja California and Sonora south to Guatemala (L. Benson, *The American Midland Naturalist* 40(1):190, 1948).

Ranunculus hydrocharoides was collected in 1970 by Mary DeDecker (*DeDecker 2501*) along the south fork of Oak Creek at 1540 m, ca. 330 m above the Owens Valley floor. In 1979, it was reported, but not collected, at two locations in Inyo Co.: Oak Creek and Bishop (Tim Nosal, California Dept. of Fish and Game Natural Diversity Data Base (NDDB), personal communication).

Smith and Berg (California Native Plant Society (CNPS), *Inventory of Rare and Endangered Vascular Plants of California*, fourth ed., 1988) placed *R. hydrocharoides* on CNPS List 2, “rare, threatened or endangered in California, but more common elsewhere.” They also stated that it occurred on the Kearsarge Peak, Bishop and Mt. Thompson 7.5 minute USGS topographic maps. D. H. Wilken (*Ranunculus* in J.

Hickman [ed.], *The Jepson Manual: Higher Plants of California*, University of California Press, 1993) noted, however, that while *R. hydrocharoides* was known from the Owens Valley, it had been "last seen in 1874." Skinner and Pavlik (eds., CNPS, *Inventory of Rare and Endangered Vascular Plants of California*, fifth ed., 1994) subsequently placed the species on CNPS list 1A, "extinct in California."

Significance. In August 1994, CNPS Assistant Botanist David Tibor alerted the lead author to the discrepancy between the 1993 Jepson Manual note and the 1979 NDBB information regarding *R. hydrocharoides*. We visited the previously noted Bishop location of this plant (Bishop USGS map) and found two small patches of it in two irrigation ditches.

Mary DeDecker visited the Oak Creek location (Kearsarge Peak USGS map) in September 1994 and reported that the site was dry due to drought; she was unable to find the previously reported patch of *R. hydrocharoides* from which she had made her collection.

It remains unclear where or if the plant has been seen in any location covered by the Mt. Thompson USGS map.

Mark Bagley had observed and collected an undetermined aquatic *Ranunculus* in Mono Co. in both 1993 and 1994, at a location 100 km north of and considerably higher in elevation than known Owens Valley *R. hydrocharoides* sites; his specimens have now been determined to be *R. hydrocharoides*.

Thus this plant is extant in California: It still exists in the Owens Valley, it extends north into Mono Co., and it may be more widespread than previously realized.

—SARA J. MANNING, 401 E. Yaney St., Bishop CA 93514; DANIEL W. PRITCHETT, P.O. Box 1411, Bishop CA 93515; and MARK O. BAGLEY, P.O. Box 1431, Bishop CA 93515.

SENECIO MIKANOIDES WALP. (ASTERACEAE)—Los Angeles Co., Angeles National Forest, San Gabriel Mts., T1N, R9W, S13, SE $\frac{1}{4}$, 460 m elev., 11 Feb. 1995, Scott D. White 2537 (UCR), verified by A.C. Sanders (UCR). San Dimas Canyon, slope just above wash above N end of San Dimas Reservoir, directly across road from US Forest Service San Dimas Station. Several well-established patches, ca. 10 m diameter, covering ground and climbing to ca. 4 m ht. in *Salix lasiolepis* and *Baccharis salicifolia*.

Previous knowledge. *Senecio mikanioides* (German ivy) is native to South Africa. It spreads aggressively in coastal California, especially in riparian vegetation, eventually covering virtually all available substrate. Known from North Coast, Central Coast, and San Francisco Bay regions <200 m elev. (T. M. Barkley 1993; p. 340 in J. C. Hickman, ed., *The Jepson Manual*) and scattered sites in the Santa Monica Mts. and San Diego Co. (Jake Sigg, personal communication).

Significance. First record from San Gabriel Mts., >60 km E from known locations in the Santa Monica Mts. Farthest inland (ca. 60 km from coast) record in California. This occurrence suggests that *Senecio mikanioides* can continue to expand its range inland from the maritime areas where it is a well known threat to native riparian vegetation.

—SCOTT D. WHITE, Tierra Madre Consultants, Inc., 1159 Iowa Avenue, Suite E, Riverside, CA 92507.

OREGON

BERBERIS DARWINII Hook. (BERBERIDACEAE).—Coos Co., scattered vigorous flowering plants on the coastline northeast of Cape Arago and southwest of the town of Charleston, T26S R14W S17, elev. ca. 20 m, in undisturbed wind-pruned coastal

scrub composed of *Gaultheria shallon*, *Vaccinium ovatum*, *Lonicera involucrata*, *Picea sitchensis*, etc., 1 April 1995, P. F. Zika 12296, B. Rittenhouse, B. Newhouse, et al. (OSC).

Previous knowledge. Native to South America, from Chile to Patagonia, Darwin's barberry is occasionally cultivated as an ornamental along the coast and in the valleys west of the Cascades.

Significance. This is the first record for Oregon as a naturalized plant. It was surely bird-dispersed to the reported locality from gardens within a few kilometers. Some shrubs were 2 meters tall and sprawling over adjacent vegetation, suggesting it has the potential to become a pest species.

—PETER F. ZIKA, Herbarium, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331.

SONORA, MEXICO

The four new records reported here are from east-central Sonora in the vicinity of Mulatos and Matarichi, approximately 14 to 20 km west of the Chihuahua border. These specimens were collected in the Sierra Madre Occidental in a region that previously had not been botanically explored. This area is remarkable for its extensive areas of hydrothermally altered soils and complex topography that provide a unique range of habitats. Despite earlier and current extensive botanical exploration farther south in the state (e.g., Gentry, Rio Mayo Plants, 1942, and Jenkins, The Revision of Howard Scott Gentry's Rio Mayo Plants, At The Pass Conference, May 1993, Borderlands Studies, University of Texas, El Paso, in press), these species have not been found farther south in Sonora, nor are they reported for the flora of Nabogame in nearby Chihuahua (Laferrière, *Phytologia* 77:102-140, 1995).

CHAETIUM BROMOIDES (Presl) Benth. ex Hemsl. (POACEAE).—Municipio de Sahuaripa, El Victor, on the Rio Mulatos, ca 3 km east of town of Mulatos, 28°39'40"N, 108°43'15"W, 920 m, east-facing hillside-riverbank just above the usual flood zone, tropical deciduous forest including *Acacia occidentalis*, *Lysiloma watsonii*, and *Montanoa leucantha*, 13 October 1994, Felger 94-414 & Bürquez (ARIZ, MEXU, UC).

Previous knowledge. Central America to Chihuahua (McVaugh, Flora Novo-Galiciana 14, 1983.).

Significance. New for Sonora, representing the northernmost record for this tropical genus.

DIGITARIA TERNATA (A. Rich.) Stapf (POACEAE).—Municipio de Sahuaripa, 1.4 mi NW of Matarachi, 28°42'05.1"N, 108°50'13.0"W, 1620 m, low hills at the northwest side of the Matarachi valley, pine-oak forest including *Quercus chihuahuensis*, *Pinus leiophylla* var. *chihuahuana*, *Juniperus deppeana*, *Ceanothus* sp., and *Agave wocomahi*, 12 October 1994, Felger 94-387B & Bürquez (ARIZ).

Previous knowledge. Durango (González et al., Listados Florísticos de México, IX. Flora de Durango, Instituto de Biología, UNAM, 1991.), Jalisco and elsewhere in the Central Plateau of Mexico. This Old World annual was apparently first collected in Mexico in 1952-1953 (McVaugh 1983).

Significance. New for Sonora. It seems unusual to find this usually weedy species in a largely undisturbed habitat in a sparsely inhabited region of the Sierra Madre Occidental far from areas of mechanized agriculture.

POUZOLZIA PALMERI S. Watson (URTICACEAE).—Municipio de Sahuaripa, 1.6 km S of Mulatos, east-west canyon draining eastward, ca. 0.5 km upstream from Proyecto

Mulatos, 28°38'30"N, 108°45'42"W, 1240 m, riparian oak woodland with some tropical deciduous forest species, e.g., *Lysiloma microphyllum*, *L. watsonii*, *Quercus chihuahuensis*, *Q. tuberculata*, *Buddleja parvifolia*, *Montanoa leucantha*; open, sparsely-branched shrubs 1.8–2.5 m tall on north-facing slope near canyon bottom, beneath *Lysiloma watsonii*, 15 October 1994, Felger 94-756 & Bürquez (ARIZ, CAS, MEXU, TEX).

Previous knowledge. Known from Sinaloa and Jalisco to Morelos (Standley, 1922, Contributions from the United States National Herbarium 23:220).

Significance. First report of the genus from Sonora. The specimen was collected from a locally extensive population, but we did not find it elsewhere in the region.

BUDDLEJA MARRUBIIFOLIA Bentham subsp. *OCCIDENTALIS* Norman (BUDDLEJACEAE).—Municipio de Sahuaripa, El Victor, on the Río Mulatos, ca 3 km east of town of Mulatos, 28°39'40"N, 108°43'15"W, 920 m, east-facing hillside-riverbank, just above the usual flood zone, with tropical deciduous forest species including *Acacia occidentalis*, *Lysiloma watsonii*, *Montanoa leucantha*; dwarf shrub, ca 40 cm tall, in crevice of rock face by river, 13 October 1994, Felger 94-428 & Bürquez (ARIZ, MEXU, UC).

Previous knowledge. This species is common in the Chihuahuan Desert, and this subspecies occurs in southwestern Chihuahua (Norman, Gentes Herbarum 10:47–114, 1967; Journal Arizona Academy Sciences 26:5–6, 1992.).

Significance. First report of this species in Sonora.

—RICHARD S. FELGER, Herbarium, University of Arizona, Tucson, AZ 85721 and ALBERTO BÜRQUEZ MONTIJO, Universidad Nacional Autónoma de México, Centro de Ecología, A.P. 1354, Hermosillo, Sonora 83000, México.

WASHINGTON

SAXIFRAGOPSIS FRAGARIOIDES (Green) Small (SAXIFRAGACEAE).—Chelan Co., Wenatchee National Forest, ca. 8 miles northwest of Leavenworth in the Alpine Lakes Wilderness, T25N, R16E, S03, elevation ca. 4300 feet, northwesterly aspect (240 degrees). Growing in Kcb garnet-biotite-quartz schist rock cliff crevices at the mouth of the Painter Creek Drainage. Numerous plants scattered over an area of ca. 500 m by 500 m, associated with *Carex rossii*, *Cheilanthes gracillima*, *Heuchera cylindrica*, *Lomatium brandegeei*, *Penstemon davidsonii*, *Phlox hoodii* and others. 15 June 1994, Harrod 391 (WTU).

Previous knowledge. Native to northern California and southwestern Oregon. First known in Washington from a popular climbing area (Burnett and Arnot 346a, 346b, WTU), and thought a possible human introduction (Gage, Madroño 39(4): 310, 1992).

Significance. Second record for Washington. The Painter Creek population is in a remote and untrafficked area, which significantly increases the likelihood that the Washington populations are naturally occurring, ca. 400 miles disjunct from the next nearest populations in southwestern Oregon.

—SARAH GAGE, Herbarium, Department of Botany, University of Washington, Box 355325, Seattle, WA 98195-5325.

COLLOMIA MACROCALYX Leiberg ex Brand (POLEMONIACEAE).—Yakima Co. Umtanum Ridge west of Priest Rapids Dam along the Columbia River, T13N R23E S04. Two patches of plants, each consisting of approximately 50 plants, past anthesis. Located on the side of a narrow, steep canyon on substrate composed of small rocks and sand derived from basalt. Basalt outcrops and talus are interfingered throughout

the area. In addition, a few plants were scattered in alluvium in the creekbed at the base of the canyon 370 m elevation. Sparse vegetation, with *Epilobium minutum*, *Eriophyllum lanatum*, *Cirsium* sp., *Bromus tectorum* and *Eriogonum niveum* present at the site. 8 July, 1994. *D. Salstrom* 9468 (WTU).

Previous knowledge. Previously thought to be endemic to Oregon, primarily in the north-central portion of the state (Joyal, Unpublished M.S. thesis, Oregon State University, 1983).

Significance. First record for Washington.

CAMISSONIA SCAPOIDEA (Torr. & Gray) Raven (ONAGRACEAE).—Kittitas Co. T16N R23E S19, 20, in large gravel deposit within 0.5 miles of the Columbia River. Sparse vegetation, with *Mentzelia laevicaulis*, *M. albicaulis*, *Eriastrum sparsiflorum* var. *wilcoxii*, *Silene cserei*, *Bromus tectorum* and *Eriogonum niveum* present in the area. Elevation 280 m. Probably ssp. *brachycarpa* (Raven) Raven, but additional specimens are required to confirm subspecies identification. 8 June, 1994. *D. Salstrom* 9469 (WTU).

Previous knowledge. *C. scapoidea* Subsp. *scapoidea*: southeastern Oregon, and central Idaho, and western and central Wyoming, western Colorado, northeastern Arizona, and adjacent New Mexico, throughout Utah, and in northeastern Nevada. Ssp. *brachycarpa*: southeastern Oregon, southwestern Idaho, northwestern Utah, and northeastern Nevada. From 850–2000 m elevation. [Raven. A revision of the genus *Camissonia* (Onagraceae). Contributions from the U.S. National Herbarium 37(5): 226, 1969].

Significance. First record for Washington.

LATHYRUS TORREYI Gray (FAGACEAE).—Pierce Co., T19N R02E S14, Porter Hills. Four small patches located in openings within a coniferous forest. Along infrequently used wildlife paths, with one patch along a maintained recreational trail. 110 m elevation. Glacial till substrate within a series of low drumlins. 21 July, 1994. *D. Salstrom, J. Gamon* 94721 (WTU).

Previous knowledge. In Washington, the taxon was known only from a few historic collections (four in Pierce County and two in Clark County) and had not been observed in the state since 1946.

Significance. The taxon was thought to have been potentially extirpated from the state [Washington Natural Heritage Program. Endangered, threatened and sensitive vascular plants of Washington. Department of Natural Resources, Olympia. 1994].

—DEBRA SALSTROM, Washington Natural Heritage Program, Box 47016, Olympia, WA 98504-7016.

OBITUARIES

VERNON IRVINE CHEADLE 1910–1995

Dr. Vernon I. Cheadle, an internationally noted research botanist and an expert on the evolution of water conducting tissue in monocotyledons, died Sunday, July 23, 1995. Santa Barbara, the botanical community, and higher education have lost a distinguished citizen and supporter.

Cheadle was raised in the dirt-poor farming community of Salem, South Dakota during the Depression; a humble beginning that help shaped his values and attitude. He attended South Dakota State College for one year, then transferred to Miami University (Ohio) graduating magna cum laude in 1932 and in 1934 completing a Master's degree. In 1936 he completed a Ph.D. at Harvard. His doctoral dissertation, under the supervision of Ralph Wetmore, was concerned with growth in monocotyledons. To Vernon's credit, his research topic was his own invention rather than an idea proposed by his advisor. Very likely an advisor would not have proposed such a wide-ranging and pioneering topic, which would have daunted a graduate student less courageous and energetic than Vernon. From his dissertation emerged widely-cited papers in 1940 and 1941, papers in which the trends of vessel origin and specialization in monocotyledons are laid out in relation to organography and systematics. Realizing that he had been able to study only a small sampling of most monocotyledon families in his dissertation work, Vernon devoted the balance of his life to investigating, in family after family, the details of vessel structure and occurrence. By extensive travel, most notably in Australia and South Africa, he obtained materials for his surveys of xylem in individual monocotyledon families. To his credit, he kept this research alive during his years as Chancellor at UCSB. A faithful attendee at national biological meetings, Vernon Cheadle presented his findings orally as well as in papers in leading journals. The most recent oral presentation of his research was a study of xylem in Bromeliaceae which was given at the Honolulu meetings in 1992 with his research assistant, Dr. Jennifer Thorsch. Thus his research career spanned more than 50 years showing that an intellectually meaningful scientific career can last a lifetime.

In 1936, Vernon joined the faculty at Rhode Island State College, serving as Professor, Chairman, and Director of the Graduate Division from 1942 to 1952, except from 1944 to 1946 when he served with the Navy in the Pacific Theater of W.W.II. In 1950–1951 he spent a sabbatical at UC Davis working with Dr. Katherine Esau, who shared his interests in phloem. The following year Vernon was invited to return to Davis as a tenured faculty member and Chair of the Botany Department. While at Davis, working in collaboration with Dr. Esau, he made significant contributions to knowledge of the structure and evolution of secondary phloem in dicotyledons, including some of the first ultrastructural studies on phloem.

Over the years, he was the recipient of numerous awards including the 1963 Award of Merit from the Botanical Society of America, of which he was President in 1961, Phi Beta Kappa, and Phi Kappa Phi. He was also a fellow of the American Association for the Advancement of Science, the California Academy of Science, and the American Academy of Arts and Science. In addition he served first as a Trustee, then honorary trustee for both the Santa Barbara Botanic Garden and Ganna Walska Lotusland.

In 1962, after serving as acting vice chancellor at UC Davis, Dr. Cheadle accepted the second Chancellorship of the University of California, Santa Barbara. Under his leadership and vision the campus underwent phenomenal growth not only in increased

number of students but also in the number of distinguished faculty, setting the foundation for the emergence of a first-class research university. Despite the riot-torn era of the late 1960's and early 1970's, marked by campus demonstrations, faculty protests, the burning of the Bank of America in Isla Vista, and mass arrests, Dr. Cheadle exhibited remarkable courage and emerged as an administrator of remarkable skill.

Dr. Cheadle retired as Professor and Chancellor Emeritus in 1977 at age sixty-seven. In 1979, the Regents of the University of California named the main administration building Vernon I. Cheadle Hall. Dr. Cheadle's associates at UCSB characterized him as: "an outstanding Chancellor whose impact was felt not only in Santa Barbara but throughout the University of California" (UC President Jack Peltason); "He never gave unwanted advice, but was thoughtful in his comments when they were solicited, and always demonstrated his deep affection for the campus he had so influenced" (Former UCSB Chancellor Barbara S. Uehling); "He was a role model for many and a wonderful human being" (Former track and field coach Sam Adams); "I always felt he was a person of integrity and principle, who understood the need to defend free expression and academic freedom. In a time of chaos, he tried to uphold the ideas of civility (UCSB Sociology Professor Dick Flacks)". Even after his retirement from the chancellor's position in 1977, Cheadle remained involved in both the university and the community it serves.

In addition to being a distinguished scientist and administrator, Vernon was an accomplished athlete. In 1978 he was inducted in the Miami Athletic Hall of Fame and for 18 years competed in the Masters Track and Field meets, holding several Masters world records in the discus and shot-put. He was a warm, friendly, unpretentious man; one of those people whose contribution is as visible and as clearly defined as the university that he helped create.

In 1990, both Vernon and his wife Mary were named honorary alumni by the UCSB alumni association for their "wise and caring leadership . . . as UCSB's first family." They were a remarkable team, dedicated to the university and community they so loved. Cheadle is survived by his wife and their son, William, an Associate Professor of Surgery at the University of Louisville.

—EDWARD L. SCHNEIDER and SHERWIN CARLQUIST, Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105.

KATHERINE K. MULLER 1909–1995

Katherine Kinsel Muller, director of the Santa Barbara Botanic Garden from 1950 through 1973, died Thursday, August 17, 1995. She was 85. Santa Barbara and the botanic garden community have lost a colleague, supporter, and friend who devoted much of her life to the vitality and visibility of public gardens. Her association with the Santa Barbara Botanic Garden began in 1948 as an associate in education. In 1950 she was appointed acting director, then named director in 1951 (see Mathias, Mildred E. 1975. Katherine K. Muller and the Santa Barbara Botanic Garden. California Horticultural Journal vol 36(2):77–78).

Katherine was an accomplished educator, administrator, and community leader. Every aspect of the Garden that we know today was influenced in some way by her early planning and guidance. Under her administrative stewardship the garden expanded to its present 65 acres, significantly increased plantings and trails for public viewing, instituted classes for adults and children, enhanced the original library by adding two wings, added a propagation complex, a two-story herbarium and research wing. During this time she taught courses on both native and introduced trees for the Garden's educational program and University of California Extension and con-

ducted travel programs, introducing many students and the general public to plant diversity and the horticultural beauty of our planet.

Katherine was born in Portland, but moved to Los Angeles with her family when she was 9 years old. She earned her bachelor's and master's degrees from UCLA and her Ph.D. from the University of Illinois. A resident of Santa Barbara since 1937, she was a botany and biology instructor at Santa Barbara State College from 1937 to 1938, and assistant professor of biology from 1943 to 1945.

Over the years, Katherine was the recipient of numerous awards for gardening, conservation, and botany, including the 1982 Eloise Payne Luquer Medal, a national award bestowed by the Garden Club of America, the Award of Merit and Commendation from the Western Chapter of the International Shade Tree Association, the Award of Merit from both the California Conservation Council and the American Association of Botanic Gardens and Arboreta.

Throughout her career, Katherine was a mentor to a loyal following of amateur and professional botanists. Her influence extended beyond botanical instruction and encouragement. She instilled dedication among her followers that led to important publications such as Cliff Smith's *A Flora of the Santa Barbara Region*, and *Trees of Santa Barbara*, co-authored with Richard E. Broder and Will Beittel. One plant was named for Katherine, *Quercus dumosa* var *kinselae*. Katherine also took the Botanic Garden to the city and the nation, participating on local boards and advisory committees as well as serving on the Board of Directors of the American Horticultural Society, the Advisory Council of the Saratoga Horticultural Foundation and Advisory Board of the Theodore Payne Foundation.

Her interest in the educational value of the Botanic Garden held steady and true through fire, flood, and drought. She was known for the serene but firm leadership, which earned praise from many local, regional, state, and national leaders. She also displayed a refined sense of humor. At a 1974 dinner at the Biltmore Hotel honoring her work, she was given an exquisite cluster of gold pine branches and pine cones. Upon accepting the gift, she paused to identify the species of pine depicted on the jewelry—in Latin.

Following her retirement, Katherine was elected Director Emeritus and continued an active role in Garden planning and programs. She served as a Garden Trustee from 1976 to 1988 and elected honorary trustee in 1989. In 1982 a reading room addition below the library was dedicated in honor of her service to the Garden. Katherine Muller contributed enormously to the quality of life in Santa Barbara and will be missed. In one way or another Katherine Muller touched our lives. We learned from her classes, enjoyed trips she led and lectures she arranged. The Garden is most fortunate to have had her as a wise and enthusiastic leader and she has left a rich legacy for us to build upon. Katherine is survived by her husband, Dr. C. H. Muller, emeritus professor of botany, University of California, Santa Barbara, and son Dr. Robert Muller, Chairman, Department of Forestry, University of Kentucky.

—EDWARD L. SCHNEIDER and MARY ALLCOTT, Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105.

REVIEWS

Species Diversity in Ecological Communities: Historical and Geographical Perspectives. By R. E. RICKLEFS and D. SCHLUTER. 1994. University of Chicago Press, Chicago. 414 pp.

What are the determinants of species richness in natural communities? This simple question, perhaps above all others, forces ecologists to confront the limits of existing theory and available data. Given the overwhelming role of cryptic and improbable quirks of history, we should find that factorial, linear and deterministic solutions are rare when explaining obvious patterns in distribution and abundance. It is not hard to notice that trees are much more diverse in the tropics than in the temperate zones, as von Humboldt did almost two centuries ago. It is also not hard to suggest a whole laundry list of possible explanations, including differences in climatic stability, productivity, competition and rates of speciation and coevolution. It is hard, however, to go beyond the list and provide synthetic, coherent and realistically detailed explanations, especially when more subtle patterns are elucidated and analyzed. Robert Ricklefs and Dolph Schlüter, along with 50 other authors, have gone beyond in this large and important book. They review old and new theory from many schools of ecological thinking, present old and new data on a wide variety of taxa and suggest the need for "a new framework for the study of diversity that emphasizes the use of comparative geographical and historical data to investigate the development of biological communities."

Toward that end, the 30 ensuing papers (including introductory and summary chapters by the editors) are divided into four major groups, reflecting a progression of spatial and temporal scales from the local to the global and from the ecological to the evolutionary. Local ecological processes, such as competition within a single habitat, were once thought only to reduce the number of species over short periods of time. But as G. E. Hutchinson suggested, temporal shifts in competitive advantage are common in nature and habitats can be finely partitioned, so that "similar" species may coexist indefinitely. Tilman and Pacala place these ideas within the most modern of contexts, emphasizing demographic, nonequilibrium perspectives that embrace the disproportionate impacts of stochastic processes. Also prominent in this section are linkages between productivity and diversity. Rosenzweig and Abramsky draw some stunning parallels between many types of modern and fossil communities, demonstrating an essentially universal pattern in space and time; diversity rises with low productivities and falls with high productivities. Importantly, they go on to discuss nine hypotheses to explain the pattern, favoring two in the end, but suggesting gaps that need to be filled with new comparative data and experimentation.

The second group of papers links processes between communities that can influence species diversity. At this "mesoscale," dispersal from one community to another (metacommunity dynamics) can allow the persistence of high levels of species richness in much the same way as dispersal between populations (metapopulation dynamics) can allow the persistence of a single species. The approach here is largely theoretical: McLaughlin and Roughgarden review several models that treat dispersal as a diffusion phenomenon influenced by competition or predation within and between collections of species. Extreme rates of dispersal, slow or fast, tend to lower mesoscale diversity, but this is greatly dependent upon environmental heterogeneity. Moderate dispersal rates among communities with patchy habitat structure tend to support larger num-

bers of species because interactions between species among all patches are less likely to all negative. This "asynchrony" allows interactions for most species to be favorable somewhere in the complex of metacommunities and thus allows for persistence. (Proponents of landscape-level efforts to conserve biological diversity should pay particular attention to these arguments.) Other models are used to explain patterns of distribution and abundance among butterflies and ten additional animal and plant assemblages (Hanksi, Kouki and Halkka), and to experiment with artificial archipelagos whose histories, phyletics and ecology can be perfectly known (Haydon, Radtkey and Pianka). What emerges from these papers is a sense of how far mathematical ecology as come over the last 20 years: model outputs have actually begun to resemble measured or observed attributes in complex communities!

Regional perspectives are covered in the third group of papers. Here, the biotas of entire continents are analyzed with respect to short-term ecological context and long-term geohistorical events. Australian communities figure prominently here, with studies of birds over large-scale transects (Cody) and comparisons with arid zone biotas in North America (Morton). In both cases, the unique history (e.g. faunal exchanges with New Guinea, antiquity of deserts) and strange phylogenetic inheritance (marsupials, Proteaceae, harvester ants) of this continent are shown to influence the patterns of alpha, beta and gamma diversity. Species-area curves even gain some respectability here, with implications for climate change and biological conservation (Westoby). I especially enjoyed the analysis of global mangrove distributions by Ricklefs and Latham, which uses fossil evidence and tectonic reconstruction to explain why the Indo-West Pacific region (including Australia) has four times the number of genera and five times the number of species as the Atlantic-Caribbean-East Pacific region. Its the kind of insightful phytogeography pioneered by R. Good (1947), but thoroughly modernized by dynamic geological and ecological principles.

The large-scale and long-term implications of phylogeny, coevolution and community development are considered in the final group of papers. At this level of analysis, modeling is replaced by cladistics, and species are replaced by guilds or higher taxa. Cornell, for example, examines the evolutionary diversification of insect guilds (e.g., sap feeders, chewing beetles) on common British trees. Surprisingly, life form characteristics of the trees (leaf longevity, palatability) did not appear to influence how many different kinds of insects contributed to guild structure. Instead, taxonomic proliferation of both insects and trees contributes to richness in a guild. *Quercus*, for example, supports excessive numbers of cynipid gall formers, not because of any particular susceptibility of oak tissues, but because both were capable of diversification in addition to coevolution. Even within the genus, the species-rich white oaks have been shown to support larger numbers of leaf miners than the species-poor white oaks. Therefore, the biogeography and history of higher taxa have influenced guild structure more than the observable, ecological features of the organisms themselves. A similar theme emerges from studies of neotropical snakes (Cadle and Greene), temperate zone trees (Latham and Ricklefs), and large North American mammals (Van Valkenburgh and Janis), thus providing support for some of Ricklefs's (1987) earlier ideas of how large-scale diversity patterns influence the structure of local communities.

I find it difficult to overstate the impact this book should have on discussions of species diversity among ecologists, graduate students and advanced undergraduates. There is a lot of meat on these bones, much more than I could gnaw off during a first reading. I also think there is much here for conservation biologists, but it is not easy to get at. Most authors stop short of developing the conservation muscles of their findings, which would have been extremely useful at the expense of editorial cohesion and another hundred, bulky pages. Nevertheless, I am left with a sense that community ecology has made some significant advances in recent years, with tremendous potential for enhancing our efforts to preserve biological diversity. This book is an excellent summary and expression of those advances.

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RICKLEFS, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167-171.

—BRUCE M. PAVLIK, Department of Biology, Mills College, Oakland, CA 94613.

Biological Diversity of Mexico: Origins and Distribution. Edited by T. P. RAMAMOORTHY, ROBERT BYE, ANTONIO LOT and JOHN FA. 1993. Oxford University Press, New York. xxxix plus 812 pp. Hardcover, \$79.95, ISBN 0-19-506674-X.

The introduction of this volume describes Mexico as the only "megadiversity" country, which is also a center of agricultural origin. With about 30,000 plant species, 1000 bird species and more than 2000 fish species, it is timely to compile at least part of the knowledge accumulated on the origin and distribution of the Mexican biodiversity.

This book is the result of a symposium on Biological Diversity of Mexico held in 1988. A large part of the biological community in Mexico and elsewhere joined in this immense effort. Twenty six chapters are divided into six main topics: historical background, description and discussion of selected faunistic groups and floristic groups (these two parts comprising more than half of the book), a section on phytogeography of selected vegetation types, one on plant diversity and humans, and finally, a review of terrestrial habitats. As in any edited book, that includes chapters produced by different authors, there is heterogeneity in quality, depth and subject matter.

The introduction to the book stresses the large number of species in the different groups encountered in Mexico and the urgent need to conserve habitats, by achieving a balance between human needs and the maintenance of biological diversity. The section on historical background starts with a description of the geology of Mexico. For the first time, a physiographic characterization is presented in association with the geologic description of the morphotectonic provinces of Mexico. Although some of the terms used may be too technical for many biologists, this chapter is a valuable source of relevant references on the geology of a particular area. The next chapter on the historical factors and the biological diversity in Mexico is a concise and well-integrated account of the different elements that have contributed to the high diversity in this country. The last chapter in this section discusses the diversity and origins of the phanerogamic flora of Mexico. Rzedowski estimates the total number of angiosperm species to be 21,600 based on the species/genera ratio of the Compositae. Data of local floras show that this ratio has a parallel with the species/genera ratio of the whole phanerogamic flora (in latitudes close to Mexico). Knowing the number of total angiosperm genera in Mexico, the number of species is estimated based on the Compositae species/genera ratio. Although interesting, this empirical relationship between ratios requires at least a hypothetical explanation to convince skeptical readers. The experienced author makes clear that the geographical distribution of endemisms does not follow the same patterns as those of diversity, which is corroborated by the evidence presented in the rest of the book.

The next section presents seven chapters on selected faunistic groups of Mexico. The chapter on native bees of Mexico is noteworthy. It goes beyond a general account of bee distribution and links the biodiversity observed with expected biogeographic patterns. A compilation of all the species recorded in Mexico is followed by a dis-

cussion of some problems detected in the collections, like the fact that they are restricted to certain seasons. Interestingly, the authors note that the diversity of bees in a region is normally well represented at specific localities, hence, intensive rather than extensive studies are recommended.

The chapter on herpetofauna of Mexico includes a brief and interesting comparison of the distribution of reptiles and amphibians in Mexico and the rest of the world. A laudable effort is made in presenting information on fossils known in this group and their correspondence with present herpetofauna. As interesting as the report on herpetofauna is the geographic, ecological and historical analysis of land bird diversity. Unweighted pair-group method analysis is used in this chapter to explain avifaunal similarity among geographic regions in Mexico. This report explains how patterns of diversity do not match patterns of endemism.

Patterns of mammalian diversity in Mexico are presented as the last chapter in this section. Mexico is reported as departing from the species-area relationship observed in mammals, indicating more mammalian species than expected based on its area. It should be noted, however, that this departure is not exclusive to Mexico, as the figure presented clearly shows. It is however refreshing to see that this comparison includes many countries, since most of the chapters compare number of species in Mexico with the number in the temperate United States or the smaller Central American countries. The conclusions reached for the patterns observed for the mammals are compared with other groups, like the amphibians, reptiles and birds, thus establishing a connection with previous chapters.

The third section in the book on selected floristic groups includes eleven chapters, starting with the diversity in the bryoflora. In spite of the scarce information available on this group, the author presents a clear idea on the origins and distribution of mosses. An important genus in Mexico: *Pinus*, is the topic covered by Styles. A clear taxonomic description is followed by a discussion on efforts geared to pine forest conservation. Also a clear taxonomic presentation as well as the first cladogram in the book is found in the report on Commelinaceae of Mexico, where karyotypic information is used to infer evolutionary dispersal. Phylogenetic relationships are also discussed in the reports on Lamiaceae and Acanthaceae. In many chapters in the book, appendices on recent literature provide interested students of the group with useful references.

The genus *Quercus* is discussed in an interesting chapter. Due to the problem presented by the use of the biological species concept in this genus rich in hybrids, the concept of phylogenetic species is used. This revision includes a discussion on fossils and biogeographic patterns. Sousa and Delgado provide a very thorough and original presentation on the Leguminosae. They divide this huge family into artificial groups according to the level of endemism. Each group is presented by discussing the distribution and origin of a few well-studied genera. An interesting account on the possible routes of migration is presented. The last chapter in this section discusses the diversity of the Mexican aquatic vascular plant flora. Due to the polyphyletic nature of this group, the emphasis given is more ecological than evolutionary.

The fourth section on phytogeography of selected vegetation types in Mexico starts with a brilliant and innovative discussion on the composition, affinities and origins of the canopy tree flora of the Atlantic rain forests. A rigorous review of recent paleofloristic data is used to shed light on the origin of the canopy flora, giving a new perspective on migration routes. This study estimates the Laurasian contribution to this flora to be at least 25%, a figure which indicates a larger ancient component of the flora than scientists have previously surmised. The second and last chapter in this section discusses the phytogeography and history of the alpine-subalpine floras of northeastern Mexico. McDonald gives a clear descriptive account of the history of this flora based on its more widespread distribution during the Wisconsin glacial, and the subsequent climatic changes that left this flora as insular refugia. He uses similarity indices to compare the affinity of this flora with that of the Rocky Mountains

and that of the Trans Mexican Volcanic Belt, concluding that the similarity is higher with the former.

The fifth section in the book on plant diversity and humans includes two chapters. The first discusses the role of humans in the diversification of plants in Mexico. Interesting concepts are presented in this chapter, such as the study of possible correlations of cultural richness with species richness. The second and last chapter of this section presents the view of Hernández Xolocotzi on some aspects of plant domestication in Mexico. This presentation touches on the origin and evolution of some cultivars through the history of Mexico, effects and perceptions of occidental science and traditional agriculture, and methods to conserve this diversity. An appendix on representative plants domesticated in Mexico is an excellent addition to this chapter.

Finally, the last section presents a clearly written review of terrestrial habitats. Toledo and Ordóñez set the ground for conservation measures, since they provide information on biological richness and endemism together with the prominent land uses in six terrestrial habitats well represented in the country. In this manner, the status of knowledge of biodiversity presented in the previous sections is united with the information on human activities in the areas where this diversity occurs.

Although few typographical errors are found in the book, a criterion on the use of accents in Spanish is lacking. More disturbing are the maps presented, where details are impossible to read.

There is no doubt that this book is overall well conceived and executed. It is a solid step towards the presentation of accumulated knowledge of the Mexican biodiversity. Anybody interested in the ecology, taxonomy, evolution, conservation or biogeography of the Mexican biota should have this volume at hand. We can only hope that the example set by this volume will be followed by future productions of equal quality. It is evident throughout this book that a lot is known about the biodiversity of Mexico, but a long path still lays ahead of us; the ignorance in many groups is vast. This book reveals that areas of richness and endemism for one group do not always coincide with that of others. Declaring all the areas of richness and endemism of every group as protected would be impossible. Greater understanding of biodiversity and of its interaction with humans can only help in the search of the balance of human needs and maintenance of biodiversity in this fascinating country.

—RENÉE GONZÁLEZ-MONTAGUT, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138.

Giant Sequoia Groves of the Sierra Nevada: A Reference Guide. By DWIGHT WILLARD. 1994. Self-published. P.O. Box 7304, Berkeley, California 94707. 372 pages.

This reference book on giant sequoia (*Sequoiadendron giganteum*) groves came about because in Dwight Willard's words, "I love sequoias." Relying on other reference materials, interviews, and personal visits to groves, Willard provides detailed information on 65 separate groves, emphasizing giant sequoia resources (location, grove characteristics, human use patterns, etc.) and natural values (noted/named trees, "other" forest, and water resources nearby). He also provides selected comments on fire history, management and research needs, and bibliographic references. Most grove descriptions are about 3½ pages long, with 12 pages in the book devoted to low quality xerox copies of USDA Forest Service or USGS quadrangle maps that show grove locations.

The book begins with an overview of the giant sequoia resource, although much of the information can also be found in Hartsveldt's (1975) "The Giant Sequoia of the Sierra Nevada" (which is infrequently cited by Willard). I was disturbed to find few other citations in the introductory material because over 3000 citations exist on giant sequoia, and appropriate credit is not given to previous researchers—especially in regards to the section on the "Physical and Biological Characteristics of the Sequoia and its Environment."

The five-page section on "Grove Management Issues" is overly simplified and leaves the impression that state and federal agencies follow one of three preservation strategies: (1) "Don't touch" management; (2) use of "controlled burning," or (3) low levels of commercial logging. I don't believe any of the three management approaches are used exclusively in any grove (by any agency). Here a discussion of ecosystem management with respect to sequoias would have been useful.

The strongest and largest portion of the book is Part 2, the grove descriptions. Here, 65 groves are described in a consistent format. The author admits (page 33) that much of the information on giant sequoia is fragmentary, unreliable, and difficult to verify. I looked more closely at the grove descriptions for three of the groves that I was most familiar with (the Big Stump, Muir, and Castle Creek groves) to assess the completeness of information offered by this reference book. The Big Stump grove is described very nicely. The description of the sequoia resources in the Muir grove missed one of the key features of the grove: the high proportion of trees in the middle size classes. The author draws attention to the larger size trees. The Castle Creek grove description claims that the grove has "virtually no scientific descriptive literature (as of May 1994)," while I am personally aware of several citations, including my own work (e.g., "Spatial patterns of giant sequoia *Sequoiadendron giganteum* in two sequoia groves in Sequoia National Park, California," Canadian Journal of Forest Research 23:120–132; 1993).

Part 3 of the book covers "selected other information" including the criteria for defining a "grove." Rundel ("An Annotated Checklist of the Groves of *Sequoiadendron giganteum* in the Sierra Nevada, California," Madroño 21:319–328, 1972) described 75 groves including isolated clusters. I preferred the longer list to the 65 groves presented by Willard because the naturally occurring small clusters may be important species range expansions in a metapopulation sense. I found "Willard's Classification of Sequoia Types" to be too teleological with terms such as "adolescent or juvenile," "young mature, or small giant," "mature" and "super giant." Age class and size class information is less ambiguous. I appreciated the author's efforts at summarizing historical logging efforts in all the groves because this has never been done. The "Selected Annotated Bibliography" listed many fine references but misses several recent and important scientific papers between 1990 and 1993. The metric system is avoided throughout the book.

In short, Willard's book falls short of being a solid scientific reference for giant sequoia groves, but it is an adequate reference for hikers and sequoia enthusiasts, and as one of many references for managers of giant sequoia groves. I admire anyone taking on the task of compiling information from such widely fragmented sources. The primary purpose of the book was to "encourage others to conduct more research, enjoy visits to the groves, and to participate in grove management planning so the giants if the Sierra Nevada forests in general can be better protected and enjoyed." Despite the issues I raise here, Willard's book is a step in the right direction.

—THOMAS J. STOHLGREN, National Biological Service, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523.

SYMPOSIUM ANNOUNCEMENT

The Santa Barbara Botanic Garden will hold a symposium entitled

PLANT EVOLUTION AND CONSERVATION ON ISLANDS—A GLOBAL PERSPECTIVE

3–5 May 1996

Topics will include phylogenetic patterns, floristic diversity, biology of rare plants, and conservation strategies. Speakers include Ian Atkinson, Bruce Baldwin, Sherwin Carlquist, Sarah Chaney, Vicki Funk, J. R. Haller, William Halvorson, and Tod Stuessy. The symposium will be preceded by a reception and open house at the Santa Barbara Botanic Garden on May 3. The full day session on May 4 will be followed by a banquet and address by Dr. Peter Raven. The symposium will be complemented by excursions to selected California Channel Islands. For details and a brochure please contact Dieter Wilken, Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105 (e-mail: wilken@lifesci.lsfc.ucsb.edu).

ANNOUNCEMENT

DESERT BOTANICAL GARDEN SELECTS NATIVE ARIZONAN AS ITS NINTH EXECUTIVE DIRECTOR

The Board of Trustees have selected Carolyn O'Malley, a native Phoenician, as the ninth executive director of the 56-year old Desert Botanical Garden. Ms. O'Malley has been serving as acting executive director since 30 September, 1994.

"It's a privilege to have this job," said O'Malley. "My top priority is to build awareness among local residents about the fantastic resource the Garden is to them. I want to change the first impression of the Garden. For the visitors, the first impression should be a fabulous botanical experience rather than a black asphalt parking lot. We hope to replace it with a new entry area including arid-plant landscaping and buildings housing our gift and plant shops."

Carolyn graduated from Phoenix Country Day School in Paradise Valley, Arizona, received her Bachelor's degree in sociology from Whittier College in southern California, and received her Master's degree in international management from the American Graduate School of International Management in Glendale, Arizona.

Prior to her appointment as acting director of the Desert Botanical Garden, Carolyn was the Garden's Assistant Director. She worked closely with staff and volunteers in the Fund Development and Community Relations departments, coordinating major gifts and special events for major donors and supervising and evaluating marketing and public relations programs designed to build greater community visibility.

She came to the Desert Botanical Garden in November, 1993, from the Volunteer Center of Maricopa County, Arizona, where she served as director of public relations for six years. Her impressive list of service to this community includes: member of the Board of Trustees both of Phoenix County Day School and the Board of Alumni of the American Graduate School of International Management; past committee member of the Valley of the Sun United Way, Valle del Sol Inc. Family Services, Emergency Services Partnership and Directors of Volunteers in Agencies. She is past board member of the Salvation Army of Glendale, Arizona and a sustaining member of the Junior League of Phoenix.

She lived in Hong Kong, Singapore, Japan, the Philippines, England, and locations from coast to coast in the United States, serving on volunteer boards and committees throughout her travels. In addition to her multicultural awareness and ability to deal with people from many ethnic groups, Carolyn converses comfortably in the Spanish language. She and her husband, Mark O'Malley, live in Phoenix.



ANNOUNCEMENT

BIBLIOGRAPHY ON FIRE ECOLOGY AND GENERAL BIOLOGY OF MEDITERRANEAN-TYPE ECOSYSTEMS.

VOLUME I. CALIFORNIA

VOLUME II. AUSTRALIA, CHILE, THE MEDITERRANEAN
BASIN, AND SOUTH AFRICA

(Bound hardcopy [ISBN 0-9626305-5-X] plus Endnote® Plus & ASCII)

Jon E. Keeley

International Association of Wildland Fire

This bibliography is a collection of the literature available on ecology, systematics, and evolution of Mediterranean ecosystems. Volume I includes 5684 citations covering chaparral, coastal sage scrub, grasslands, vernal pools, woodlands, montane forests, and interior Rocky Mountain chaparral. Volume II includes 3060 citations. The data bases are divided into chapters, but are readily utilized as a single data base for keyword searches. Endnote® Plus bibliographic format allows for easy searches and customized citation formats as well as other bibliographic features. Users not having Endnote® Plus can use the data base in Wordperfect® or other systems capable of importing an MS-DOS® ASCII file, or for a nominal fee, obtain a README-only copy of Endnote® Plus.

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PRESIDENT'S REPORT FOR VOLUME 42

Welcome to the Society's 1995-1996 program year! The Council has prepared an exciting agenda for the year, including a series of interesting monthly programs, the annual banquet, and the biennial Graduate Student Meeting. The monthly meeting and guest presentations will be held on the third Thursday of the month, at 7:30 p.m., in Valley Life Science Building (VLSB) on the Berkeley campus (the program has been mailed to members). Continuing our tradition started last year, each meeting will be followed by a reception in the lobby of the University and Jepson Herbaria on the lower floor of VLSB. We want to stimulate increased attendance at the meetings and interest in our program, so we encourage all members, friends, and other interested individuals to come whenever possible. Please post the list of speakers and the announcements of the banquet and Graduate Student Meeting.

The Council also is pleased to announce that this year's banquet will be held in southern California at Rancho Santa Ana Botanic Garden (RSA). Mark Porter, our Second Vice-President, is making the arrangements. Ken Berg said he is honored to be this year's speaker, and will be traveling from his busy schedule as BLM's Chief Botanist in Washington, D.C., to make his presentation: *Conservation of Native California Plants in the Changing Political Landscape*. Ken promises to provide an up-to-date and timely accounting of the challenging situation. We enjoyed a successful banquet in Santa Cruz last year and received an enthusiastic and insightful presentation from Mary Barkworth. Thanks again to Dean Taylor for organizing the event, and to Mary for visiting with us.

Lisa Schultheis is the Graduate Student Representative on the CBS Council and is responsible for much of the organization of the Graduate Student Meeting. She has included an initial announcement to stimulate early interest. Please post the flier and circulate it among your students. We look forward to a well-attended and successful event. Continuing another tradition started a few years ago, the Meeting will be held on the same day and at the same institution as the banquet. In an effort to provide greater interaction between the northern and southern botanical "communities" in California, we feel it is important to recognize that the future of the Society rests in a state-wide effort. Thus holding the banquet and Graduate Student Meetings at RSA should help achieve our goals as the California Botanical Society. We will send a mailing regarding the details later in the year.

At this time, I also take the opportunity to announce that the Council is looking for replacements for the positions of Treasurer and Corresponding Secretary. Margriet Wetherwax and Holly Forbes graciously agreed to stay on for a fourth year while we look for their replacements for the three-year commitments. The Council included job descriptions with the program mailing for both these very important and demanding volunteer positions. Please contact Holly (510-643-8040) at the University Botanical Garden for details on the duties of the Treasurer and Margriet (510-643-7008) at the University and Jepson Herbaria for details on the duties of the Corresponding Secretary.

Additional copies of the Jepson Symposium volume of *Madroño* (42:2) are available @ \$20.00. We are quite proud to have been able to provide this important issue with the financial support of The Friends of the Jepson Herbarium. The issue has been referred to as the agenda for botanical investigation and prioritizing in California as we head into the next millennium. Please send your requests and checks to the Treasurer.

I look forward to seeing many of you throughout the year! Thanks for your continuing support of the California Botanical Society.

—WAYNE R. FERREN, JR., President, CBS.

EDITOR'S REPORT FOR VOLUME 42

This report serves to tell members of the Society the status of Madroño from manuscripts submitted to papers published. Since the previous editor's report (see Madroño 41(4)) the journal received 67 manuscripts for review, including Articles, Notes, and Noteworthy Collections; 41 of these have since been accepted for publication. Average turn-around time for articles from submission to acceptance was 5.5 months. Notes generally took less time, and Noteworthy Collections generally appeared in the first issue available. Time between acceptance and appearing in print ranged from 3 to 8 months. As was the case last year, very few manuscripts were rejected outright or after review. Authors of Madroño articles did a fine job of responding to reviewers' suggestions.

This year volume 42(2) was a special issue dedicated to a symposium on *The Future of California Floristics and Systematics*, held at Berkeley in June of 1994. While assembling an ordinary issue of Madroño takes considerable coordination, assembling a large symposium issue was truly an organizational adventure. I thank in particular all of the authors for trying to adhere to a tight schedule, and all of the persons whom I enlisted to cajole authors to stay on schedule. The result, I think, was worth the effort, as it gave Madroño a new kind of visibility as a forum for addressing the problems and goals of studying the flora of California. Two persons merit acknowledgement for their roles in the symposium issue: Brent Mishler, who first suggested to me that Madroño might be a good place for publishing the proceedings, and who twisted more than a few arms of authors; and Susan D'Alcamo, who was the chief facilitator of the symposium and who interacted early with participants who eventually became authors.

Finally, I thank especially an array of persons who have made my job as editor easier, including: Jon Keeley, who continues to serve as book review editor; Kristina Schierenbeck, a particularly active member of the editorial board; Steve Timbrook, who assembles the Index and Table of Contents; Sheila Johnson, my student assistant who is really the reason that Madroño publication turn-around time is as short as it is; Jim Kelley, Dean of the College of Science at SFSU, who provides the funds to support Sheila; Annielaurie Seifert at Allen Press for taking the worry out of editing; members of the CBS executive council for buffering me from all non-editorial Madroño matters; and lastly the numerous reviewers upon whom I depend so much for their counsel—their names appear on a separate page of this issue.—Robert Patterson

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Published quarterly by the
California Botanical Society, Inc.
Life Sciences Building, University of California, Berkeley 94720

Printed by Allen Press, Inc., Lawrence, KS 66044



DEDICATION

Howard Latimer, Professor Emeritus of Botany, California State University, Fresno has distinguished himself as a highly respected teacher and mentor to students at CSU Fresno since 1958. After having had the unusual experience of working for both Rexford Daubenmire and R. H. Whittaker during his master's work at Washington

State University, he obtained his Ph.D. working with Verne Grant at the Claremont Graduate School in 1958 where he conducted classic work on the breeding system and evolutionary ecology of two species of *Gilia*. His research interests while at CSU Fresno have focused on the ecology of Central Sierra Nevada species with an emphasis on fire ecology and reproductive biology. His collaborative research with students has earned him the reputation of an expert on the central California endemics, *Carpenteria californica* and *Collomia rawsoniana*. Dr. Latimer regards himself first as a teacher and has found one of his most pleasurable challenges to encourage an interest in botany where there previously was none. Dr. Latimer has served as an inspiration to students through his dry wit and unselfish encouragement. Students from his courses during thirty-five years of teaching uniformly report of his infectious love of botany, evolution and evolutionary ecology. Many of his students have gone on to become influential college professors, teachers of grade through high school, conservationists, and agency botanists. They are located throughout the U.S. and in many cases are vitally involved in determining public conservation policy. It is with great appreciation and warmth of heart that we dedicate this volume to Dr. Howard Latimer.

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DATES OF PUBLICATION OF MADROÑO, VOLUME 42

Number 1, pages 1–91, published 25 April 1995
 Number 2, pages 93–306, published 16 May 1995
 Number 3, pages 308–425, published 6 October 1995
 Number 4, pages 426–540, published 17 January 1996

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